

CYTOGENETIC STUDIES OF AN INVERSION IN MAIZE¹W. A. RUSSELL² AND C. R. BURNHAM³

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In higher plants, pollen sterility frequently has been found to be the result of abnormal chromosome behaviour or of structural changes in the chromosomes such as translocations, inversions and deficiencies. The degree of sterility may vary from low to high and may or may not be associated with the same degree of ovule abortion, depending on the nature of the abnormality and the species. These changes may occur naturally, or may be induced by X-rays or other irradiations. This is a report of studies in corn, *Zea mays*, of an X-ray produced stock which shows a low degree of pollen abortion without corresponding ovule abortion.

In maize, pollen sterility due to heterozygous reciprocal chromosomal translocations is accompanied by approximately the same degree of ovule abortion, usually about 50 per cent, Brink and Burnham (2), Burnham (5), although some with only about 25 per cent have been reported, Burnham (4) Clarke and Anderson (8), Clark (7). The former have at diakinesis a ring of four chromosomes plus eight pairs most frequently; while the latter have a chain of four chromosomes plus eight pairs as the usual configuration as the result of one break being in the satellite. In the latter it was suggested that the deficiency for a piece of the satellite in one of the classes which normally aborts fails to cause abortion, thus giving 25 per cent of sterility rather than 50 per cent. This class was shown to be functional in female gametes, Burnham (4).

Pollen sterility in maize, not accompanied by an equal amount of ovule abortion, has been reported rather infrequently. A gene for pollen abortion *pa* has been reported in an inbred line by Burnham (6). Plants heterozygous for this gene produced semi-sterile pollen, but normal ears. As this gene is lethal to pollen carrying it, but not to ovules, *pa* is transmitted mainly, possibly entirely, through the ovules. Genetic data placed *pa* in chromosome 1 but no cytological abnormality could be located although it was pointed out that a very small deficiency might not have been recognizable.

Clark (7), in studying the causes of partial sterility in inbred lines and hybrids of corn, investigated pollen and ovule semi-lethals in which semi-sterility is a result of gene action rather than of chromosome aberrations. One of these types produced pollen which was 30 per cent aborted but had normally filled ears. A cytological examination of the chromosomes showed that they were all apparently normal. She suggested that there could have been a chromosomal aberration present, so small that it was not detected in the cytological examinations.

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In the same study she found one inversion which caused low pollen and ovule sterility. This inversion was of the pericentric type which includes the centromere. A second inversion of the paracentric type which does not include the centromere was reported but the amount of male and female sterility was not given.

McClintock [unpublished observations cited by Smith (15)] has observed that inversions (and other aberrations which give rise to bridge configurations at meiosis) do not produce female sterility proportionate to the number of anaphase cells with bridges. In her reports (13, 14), she has not given the pollen and ovule abortion in plants heterozygous for the inversions.

Smith (15) reported an inversion in a strain of barley. One plant, at the first meiotic division of the pollen mother cells, had 24 per cent of the cells with either a bridge or both a bridge and a fragment, while a second had 14 per cent. Female fertility was not much reduced in the first plant, there being a seed in all but one of 45 primary florets.

Sturtevant and Beadle (18), in a study of inversion heterozygotes in *Drosophila melanogaster*, suggested a possible explanation for the absence of inviable zygotes resulting from single crossovers in the inverted segment. Meiosis in the oocytes results essentially in a linear quartet of nuclei. A single crossover in the inverted section during the first meiotic division results in a dicentric chromatid which forms an anaphase bridge. At the second division this bridge is assumed to hold the crossover chromatids together and only the non-crossover ones are free to move into the terminal nuclei. Since it is always one of these terminal nuclei that functions as the egg nucleus, it is evident that only a non-crossover chromatid can be recovered, and no egg sterility would be observed. Since there is a linear quartet of megaspores in maize, a similar result might be expected.

DESCRIPTION OF STOCK AND RESULTS OF FIRST STUDIES

The partially sterile line of maize used in this study came from a culture grown from seed* produced by the application of X-rayed pollen on a normal plant. It was one of a group showing partial pollen sterility and 10 pairs of chromosomes at diakinesis which had been selected in 1940 during a search for new translocations involving chromosome 6. It was designated as sterile line number 6071.

The original plant from which this culture came had an estimated 15 per cent of its pollen grains wholly or partially devoid of starch while the ear appeared normally filled. The breeding behaviour in later generations was checked in progeny from the selfing of partially sterile plants and also from crosses with normals using them as the male and as the female parents. In the progeny derived from selfing, about 50 per cent of the plants had partially sterile pollen. In the progeny of crosses with standard normals using a partially sterile plant as the female parent, about 35 per cent of the plants from one cross and about 50 per cent from a second were classified as partially sterile. When crossed as the male parent, about 50 per cent of the progeny in two crosses and about 30 per cent in a third cross were "low sterile" plants. As before, examination of the ears

*Furnished by L. J. Stadler.

indicated that the abnormality did not cause ovule abortion. Since the sterility was transmitted through both male and female, plants with normal pollen from a cross of low sterile $\times$ low sterile were self-pollinated and crossed with a standard normal line as a test to determine if a stock homozygous for the abnormality could be established. Cytological examination of microsporocytes of partially sterile plants revealed 10 pairs of chromosomes, all apparently normal at diakinesis. Also the spore quartets were normal as to nucleolar appearance (one per spore).

Partially sterile plants were crossed with genetic markers in the various linkage groups and the partially sterile F_1 plants were backcrossed to the normal recessive stock. At this point the first writer took over the study, conducted the linkage tests, the pachytene analysis of the abnormality and further pollen sterility studies.

Pollen examination of the test crosses to establish a stock homozygous for the abnormality showed six crosses with all normal plants and five crosses with all low sterile plants. Consequently, about 50 per cent of the normal plants from low sterile 6071 $\times$ low sterile 6071 were actually homozygous for whatever produced the low sterility character. Pollen counts to determine the amount of abortion were made on these same plants and are in Table 1. In general, there was a clear-cut division between sterile and normal grains, although a few smaller, almost completely filled, grains were present in each sample. In these progenies, the variation in sterility between plants within a cross was rather small, and was not much greater between progenies. A certain amount of variation is expected due to environment and to sampling from the anther. Progeny A5730 was studied for the variation between florets within a single plant. This variation was found to be quite small, ranging only from 16.3 per cent to 19.4 per cent. For all the plants, pollen abortion varied from 12 to 22 per cent, the average being 16.5.

The proportions of low sterile plants in the various progenies of crosses between low sterile and normal plants, omitting those where there may have been disturbances due to linkage of mutant characters with the

TABLE 1.—POLLEN COUNTS OF F_1 PROGENY FROM CROSSES OF STANDARD NORMAL LINES $\times$ LINES HOMOZYGOUS FOR THE CAUSE OF THE LOW POLLEN STERILITY (No. 6071)

Progeny	Number of normal grains	Number of aborted grains	Total	Percentage aborted	Average
A5730-1	5480	1192	6672	17.9	18.5
-2	1977	468	2445	19.1	
-3	753	208	961	21.6	
A5731-1	944	142	1086	13.1	12.6
-2	816	111	927	12.0	
A5734-1	1178	176	1354	13.0	12.7
-2	1055	150	1205	12.4	
A5735-1	955	197	1152	17.1	15.9
-2	1398	284	1682	16.9	
-3	873	127	1000	12.7	
A5736-1	901	173	1074	16.1	16.1
-2	796	152	948	16.0	
Totals	17,126	3380	20,506		16.5

TABLE 2.—DATA ON BRIDGES AND FRAGMENTS AT THE FIRST MEIOTIC DIVISION IN POLLEN MOTHER CELLS OF LOW STERILE F_1 PLANTS FROM A CROSS OF STANDARD NORMAL $\times$ HOMOZYGOUS LINES

Total sporocytes	Bridge		No bridge		Per cent irregular cells
	Fragment	No fragment	Fragment	No fragment	
53	24	15	Early anaphase I 0	14	73.6
33	6	5	Late anaphase I 2	20	39.4
216	14	5	Telophase I 34	163	24.5
Total 302	44	25	36	197	26.5

sterility, varied from 25.7 to 70.4 per cent for progenies of individual ears, many of the deviations from 50 per cent being highly significant. The percentage on the total, however, was 49.3. All of the progenies but one, which had 65.3 per cent of low sterile plants, resulted from crosses using a partially sterile plant as the female parent.

CYTOLOGICAL RESULTS

Although the cytological results were not obtained until after the first linkage tests were completed, they will be presented first since they indicate the kind of change which had occurred. All cytological work was done at University Farm, St. Paul. For this study plants homozygous for the change producing sterility 6071, plants heterozygous for it, and standard normals were grown at University Farm, St. Paul, in the greenhouse. The sporocytes were killed and fixed in three parts 95 per cent ethyl alcohol and one part glacial acetic acid, and later transferred to 70 per cent ethyl alcohol for storage in the refrigerator. The aceto-carmin smear technique was used for cytological examinations. Camera lucida drawings, magnified $4500\times$ on the paper, were made of a number of cells exhibiting chromosome abnormalities. Photographs of three of these drawings, reduced 20 per cent, are presented here.

The fact that the sterility was present in the male and not in the female, but was transmitted through both, suggested that an inversion might be present in one of the chromosomes. Consequently, emphasis was placed on a study of the pachytene and anaphase stages of meiosis. A few preparations of diakinesis and metaphase I were examined but, in accord with the earlier observations, no irregularities were seen.

Anaphase and telophase stages of the first meiotic division showed a number of cells each of which contained a bridge and a fragment. Counts made on these irregularities are given in Table 2. They are based on three slides from two plants of progeny A5735, all of which should have been similar. The presence of the bridges and fragments indicates the presence of an inversion which does not include the centromere, i.e. the paracentric

TABLE 3.—DATA ON FRAGMENTS AT THE SECOND MEIOTIC DIVISION IN POLLEN MOTHER CELLS OF LOW STERILE F_1 PLANTS FROM A CROSS OF STANDARD NORMAL $\times$ HOMOZYGOUS LINES

Total cells	Fragment	No fragment	Per cent irregular cells
167	16	Metaphase II 151	9.6
24	5	Anaphase II 19	20.8
134	16	Telophase II 118	11.9
Total 325	37	288	11.4

type. The bridge plus fragment configuration at anaphase I is the result of a single crossover or of a 3-strand double crossover within such an inversion. Two-strand double crossovers do not result in bridges and fragments since the chromatids are normal. On the other hand, a 4-strand double crossover is expected to give rise to two bridges plus two fragments at anaphase I. No double bridges were identified in heterozygous 6071, suggesting that very little double crossing over occurred within the inverted segment.

The chromatids having a single crossover, whether from an actual single crossover, or from 3- or 4-strand doubles, carry chromosomal duplications and deficiencies and in seed plants are expected to result in aborted spores. The degree of pollen sterility should be related to the frequency of crossing over. Sibs of these plants grown in the field had 15.9 per cent pollen abortion. If, on the average, only two cells of a quartet in which crossing over has taken place develop into normal pollen grains, the number of cells expected to show abnormalities at anaphase I would be 2×15.9 or 31.8 per cent. A much higher proportion of abnormalities than this was observed at anaphase I. The number observed at telophase was considerably less. The number of cells on which the anaphase observation is based was very small; also certain late disjunctions with no fragments may have been erroneously recorded as bridges. A closer relation might have been obtained if pollen counts had been obtained on the plants examined cytologically (grown in the greenhouse), but unfortunately the entire tassel was taken for sporocytes. The camera lucida drawing shown in Figure 1 is typical of cells which showed anaphase bridges and fragments during the first division. It will be noted that the size of the fragment is rather large as compared with the size of the chromosomes. In many cases, the bridge had been broken before reaching telophase I.

Counts made on abnormalities in division II are shown in Table 3. It is readily seen that the number of cells with fragments at division II is considerably less than the number with bridges and fragments in division I. This may be due to the association of the fragment with a normal chromatid in the bridge figure as observed by McClintock (14). No bridges were seen in any of the second division figures. As shown by McClintock (14), these occur when certain strands cross over between the centromere and the

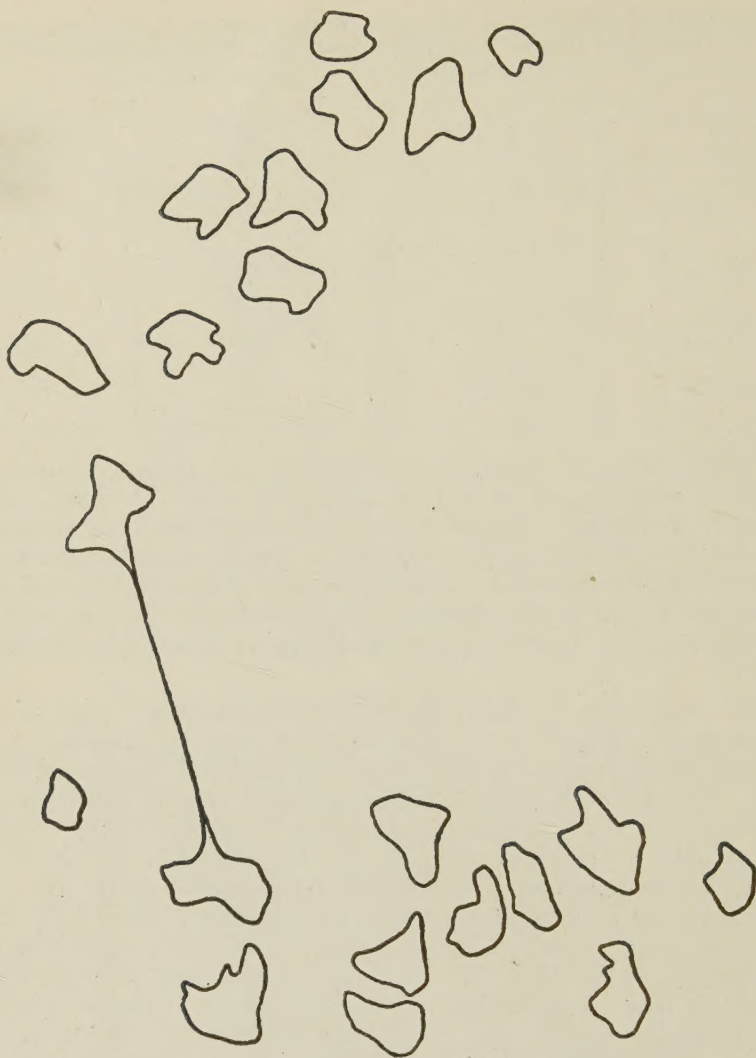


FIGURE 1. Camera lucida drawing (X 3600) of anaphase I in a plant (heterozygous for an inversion in the long arm of chromosome 2.) Note the single bridge and free fragment.

inversion loop simultaneously with certain single crossovers within the loop. Since no anaphase II bridges were seen, such simultaneous crossovers must have occurred infrequently if at all.

A large number of pachytene cells was examined for the pairing behaviour of the chromosomes. Very few cells were obtained with the proper staining of chromosomes to show individual members of a pair. During these observations, chromosomes 1, 3, 6, 7, 8, 9, and 10 were identified, and they appeared to be normal in all respects. Six configurations were seen which were similar to the inversion figures presented by McClintock (13, 14). Measurements taken on the chromosome concerned

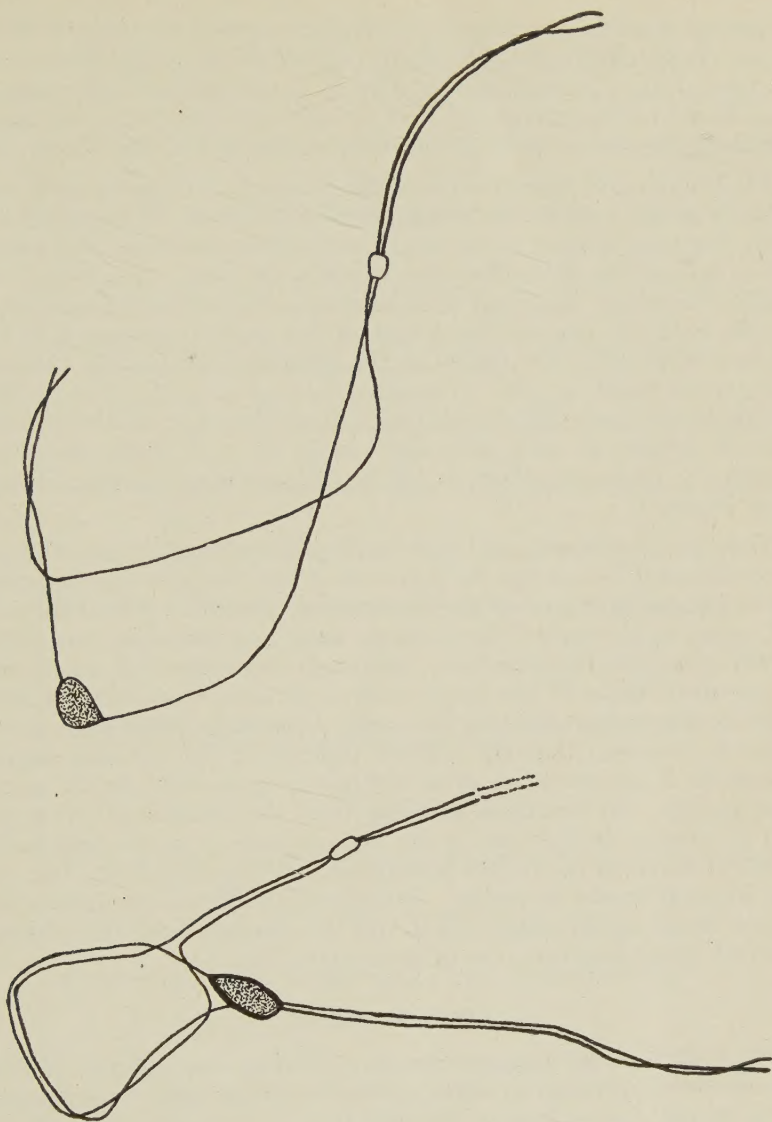


FIGURE 2 (*Top*). Camera lucida drawing (X 3600) showing asynapsis of a normal chromosome and its homologue possessing the inversion. The clear oblong area is the centromere.

FIGURE 3 (*Bottom*). Camera lucida drawing (X 3600) showing synapsis at pachytene of a normal chromosome and its homologue possessing the inversion.

and a comparison with other chromosomes indicated it was chromosome 2. In all cases but one, the region involved was in the long arm between the subterminal pycnotic body and the centromere (Figure 3). This one exception, shown in Figure 2, probably exhibits asynapsis of homologous parts at the distal side of the pycnotic body. Measurements of the loop and the long arm showed that about 50 per cent of the total length of that

arm was involved in the inversion. Unfortunately, in none of the cells were the chromomeres stained clearly so that all the single strands at the cross were distinct enough to be seen in a photograph. However, the loop could not be mistaken because of the characteristic shape and position of the knob, the size of the loop and the location of the centromere.

The lengths and relative sizes of the products of crossing over may be calculated on the basis of the breakage point locations. The length of the acentric fragment is equal to the length of the pachytene loop plus twice the length of the portion of the long arm distal to the loop. The length of the dicentric chromatid, based on a standard cytological map where number 10 is 100, is 242.5, whereas the length of the acentric chromatid is 149.5. Associated with each centromere of the dicentric is a normal chromatid, the length of which is 196. Therefore, placed on a relative pachytene length basis, the normal chromatid plus half the dicentric, or $196 + 242.5/2 = 317.25$, will be at each pole and should be 2.1 times the acentric chromatid, or fragment, which is 149.5. This is roughly what it appears to be in Figure 1.

A few slides were prepared from anthers of the homozygous 6071 plants to determine whether or not the positions of the breaks in the chromosome could be located by means of the chromomere pattern. Chromosome 2 in the X-rayed stock carried the pycnotic body and therefore this region is expected to be with the inversion. Although chromosome 2 was identified with certainty twice in the large number of cells examined, no distinct changes in chromomere pattern indicating a breakage point were seen. It was noted, however, that the relative position of the pycnotic region in chromosome 2 appeared the same for homozygous 6071 as for standard normal plants. On this basis and also from the location of the pycnotic region in relation to the loop in the heterozygote, it seems reasonable to conclude that one of the breaks is near this dark staining body, but that it is not included in the inversion. Measurements of the pachytene figures place one break at approximately 0.1 of the distance from the centromere to the end of the long arm, the other at about 0.6.

LINKAGE TESTS

The field tests for linkage were made during the summer of 1946 at the Dominion Experimental Station, Morden, Manitoba. Supplementary data for linkage group 2 were obtained from backcross progeny grown at the University Farm, St. Paul, Minnesota, during the summer of 1947. The crosses involved the tester characters for the ten linkage groups as shown in Table 4. The positions of the genes and the probable positions of the centromere (S.F.) in the linkage map are also shown, based on Anderson and Randolph (1). The end of the map nearest the end of the short arm of the chromosome is at the left. Only in group 2 were both arms adequately tested. In group 5, the crosses made to give segregation for a_2 and bm showed no segregation for sterility. Usually two or three backcrossed ears were tested for each group. Enough seed was planted to furnish a planned minimum of 400 plants for each linkage group. Unfortunately, adverse weather conditions after planting in May caused very poor germination in certain classes, particularly sugary and shrunken

TABLE 4.—LIST OF GENES USED AS TESTERS FOR EACH LINKAGE GROUP, TOGETHER WITH THEIR MAP LOCATIONS AND THAT OF THE CENTROMERE (S.F.), THE LATTER BASED ON ANDERSON AND RANDOLPH (1)

Linkage group	Name of gene used and symbol, and respective chromosome maps*					
1	<i>bm₂</i> —brown midrib-2, <i>br</i> —brachytic, <i>f</i> —fine stripe-1, <i>P</i> —pericarp and cob colour.					
	<i>P</i>	S.F.	<i>br</i>	<i>f</i>	<i>bm₂</i>	
	28	— —	86	91	166	
2	<i>B</i> —plant colour booster, <i>gl₂</i> —glossy seedling-2, <i>lg</i> —ligueless leaf-1, <i>v₄</i> —virescent seedling-4, <i>Ch</i> —chocolate pericarp.					
	<i>lg</i>	<i>gl₂</i>	<i>B</i>	S.F.	<i>v₄</i>	<i>Ch</i>
	11	30	49	—	82	124
3	<i>a</i> —aleurone, plant, and pericarp colour-1, <i>na</i> —nana-1, <i>ts₄</i> —tassel seed-4.					
	S.F.	<i>ts₄</i>	<i>na</i>	<i>a</i>		
	— —	55	83	111		
4	<i>gl₃</i> —glossy seedling-3, <i>su</i> —sugary endosperm-1, <i>Tu</i> —tunicate ear.					
	<i>su</i>	S.F.	<i>Tu</i>	<i>gl₃</i>		
	71	—	107	118		
5	<i>A₂</i> —aleurone colour, <i>pr</i> —red aleurone, <i>v₂</i> —virescent seedling-2.					
	<i>a₂</i>	S.F.	<i>pr</i>	<i>v₂</i>		
	0	—	31	72		
6	<i>Pl</i> —purple plant colour, <i>su₂</i> —sugary endosperm-2**, <i>Y</i> —yellow endosperm.					
	S.F.	<i>Y</i>	<i>Pl</i>	<i>su₂</i>		
	— —	13	41	49		
7	<i>gl</i> —glossy seedling-1, <i>ra</i> —ramosa ear-1, <i>v₅</i> —virescent seedling-5.					
	<i>v₅</i>	S.F.	<i>ra</i>	<i>gl</i>		
	24	—	32	36		
8	<i>j</i> —japonica-1, <i>ms₈</i> —male sterile-8.					
	S.F.	<i>ms₈</i>	<i>j</i>			
	— —	14	28			
9	<i>C</i> —aleurone colour, <i>sh</i> —shrunk endosperm, <i>wx</i> —waxy endosperm.					
	<i>C</i>	<i>sh</i>	<i>wx</i>	S.F.		
	21	24	54	—		
10	<i>g</i> —golden, <i>R</i> —coloured aleurone and plant.					
	S.F.	<i>g</i>	<i>R</i>			
	— —	43	57			

* Hayes and Immer (11), Emerson *et al.* (10).** The position of *su₂* is not certain; Burnham (unpublished data) reported it to be 7.7 units to the right of *Pl*, while Horovitz *et al.* (12) reported it to be 7.4 to the left of *Pl*.

TABLE 5.—DATA ON THE SEGREGATION OF PLANTS WITH NORMAL AND WITH PARTIALLY STERILE POLLEN IN RELATION TO GENES IN THE TEN LINKAGE GROUPS, TOGETHER WITH THE P VALUES FOR χ^2 TESTS FOR INDEPENDENCE—BACKCROSS DATA

Linkage group	Genes tested		Normal pollen		Partially sterile pollen		Total plants	Number of progenies	χ^2 values	P values
	X	x	X	x ²	X ²	x				
1	<i>Bm</i> ₂	— <i>bm</i> ₂	115	92	73	57	337	4	0.01	0.90
	<i>Br</i>	— <i>br</i>	112	93	67	63	335	4	0.31	0.50
	<i>F</i> ₁	— <i>f</i> ₁	117	89	74	55	335	4	0.01	0.90
	<i>P</i>	— <i>p</i>	88	82	45	48	263	4	0.27	0.50
2	<i>B</i>	— <i>b</i>	52	89	110	53	304	3	28.45	0.001**
	<i>Ch</i>	— <i>ch</i>	41	32	39	54	166	1	3.32	0.06
	<i>Gl</i> ₂	— <i>gl</i> ₂	60	82	90	72	304	3	3.36	0.02–0.05*
	<i>Lg</i> ₁	— <i>lg</i> ₁	66	76	80	82	304	3	0.26	0.05
	<i>V</i> ₄	— <i>v</i> ₄	24	118	139	23	304	3	143.98	0.001**
3	<i>A</i> ₁	— <i>a</i> ₁	40	108	41	92	281	6	0.49	0.30
	<i>Na</i> ₁	— <i>na</i> ₁	44	12	37	23	116	2	3.93	0.02–0.05*
	<i>Ts</i> ₄	— <i>ts</i> ₄	64	35	51	50	200	3	4.10	0.02–0.05*
4	<i>Gl</i> ₃	— <i>gl</i> ₃	90	45	98	33	266	3	2.13	0.10
	<i>Tu</i>	— <i>tu</i>	31	52	12	23	118	2	0.10	0.70
	<i>Su</i> ₁	— <i>su</i> ₁	70	13	26	9	118	2	1.64	0.20
5	<i>Pr</i>	— <i>pr</i>	122	78	81	48	329	7	0.11	0.70
	<i>V</i> ₂	— <i>v</i> ₂	67	35	83	57	242	1	1.03	0.30
6	<i>Pl</i>	— <i>pl</i>	6	1	25	8	40	1	0.01	0.95
	<i>Su</i> ₂	— <i>su</i> ₂	86	93	80	73	332	2	0.59	0.30
7	<i>V</i> ₅	— <i>v</i> ₅	53	39	112	81	285	3	0.01	0.90
	<i>Ra</i>	— <i>ra</i>	62	27	136	54	279	3	0.11	0.70
	<i>Gl</i> ₁	— <i>gl</i> ₁	63	29	136	57	285	3	0.12	0.70
8	<i>Ms</i> ₈	— <i>ms</i> ₈	27	—	43	—	70	1	3.66	0.05–0.10
	<i>J</i> ₁	— <i>j</i> ₁	32	10	46	9	97	2	0.84	0.30
9	<i>C</i>	— <i>c</i>	49	18	43	17	127	2	0.03	0.80
	<i>Sh</i>	— <i>sh</i>	84	34	70	37	225	3	0.86	0.30
	<i>Wx</i>	— <i>wx</i>	104	76	73	52	305	4	0.01	0.90
10	<i>R</i>	— <i>r</i>	26	6	67	51	150	2	5.40	0.02 ¹ –0.05 ^{1*}
	<i>Gl</i>	— <i>gl</i>	20	6	50	40	116	1	3.01	0.05–0.10 ¹
?	+	— —								
		aleurone ²	94	112	62	67	335	4	0.19	0.50
		"	70	72	84	77	303	3	0.07	0.70
		"	65	83	65	66	279	6	0.91	0.30
		"	59	42	58	60	219	2	1.88	0.10
		"	14	28	23	32	97	2	0.75	0.30
?	Y	— <i>y</i> ⁴	49	18	43	17	127	2	0.03	0.80
		"	73	73	32	43	221	3	1.07	0.30
		"	33	59	70	123	285	3	0.00	0.90

¹ Continuity correction applied.² Parental classes except for *P*, *Ch* and *Tu*.³ + and — = coloured vs. colourless aleurone.⁴ Probably *Y* — *y* in chromosome 6 but not certain.

* Significant.

** Highly significant.

endosperm in groups 4 and 9, respectively. Even with supplementary seedlings made the second week in June, the numbers still did not reach the number planned, but are believed sufficient in most cases to detect the presence of anything but very loose linkage.

Crosses segregating for seedling characters were classified early after emergence; the recessives which would not be recognizable later were staked and rechecked several times. After complete emergence, individual plant notes were taken. Thereafter, the segregation for plant characters was recorded at the time when they became most apparent. In most cases, the tester characters could be classified in advance of maturity so that the late-seeded material was as useful as that seeded earlier.

A pollen sample from each plant was examined to determine whether it was normal or partially sterile. For this purpose, a small piece of the tassel ready to shed pollen was collected, an anther teased out in iodine-potassium iodide solution on a slide and examined with a binocular microscope. Any sample with over 5 per cent of empty or only partly filled grains was classified as partially sterile. After first counting and estimating a few samples to ascertain the characteristic appearance, the classifications were made by estimation.

After all field characters were recorded and the pollen samples classified, the data were assembled and grouped to test for linkage using the chi-square (X^2) test for independence, by use of the formula

$$X^2 = \frac{(ad - bc)^2 N}{(a + b)(a + c)(b + d)(c + d)} \text{ with one degree of freedom.}$$

The progenies in the group showing linkage with pollen sterility were tested for heterogeneity by the X^2 method. P values smaller than 0.05 are considered significant and smaller than 0.01 highly significant. Where association was indicated recombination values were calculated.

A summary of the data for the four phenotypes involving pollen sterility and each qualitative genetic character is given in Table 5. A similar summary of data in which the particular genes responsible for the genetic characters are not definitely known, aleurone and endosperm colours, is in the latter part of this table. For all except *Tu* in group 4, *P* in group 1, and *Ch* in group 2, partial sterility entered the cross with the dominant character. Hence, with these exceptions, X sterile and x normal are the parental classes.

The P values given in Table 5 indicate that, with the exception of groups 2, 3, and 10, there is no association between pollen sterility and the genes tested. In linkage group 1 (*bm*, *br*, *f*, *P*), the total number of plants used to test the P vs p genes was less than for the other genes because of a heavy smut epidemic on ears. In group 4 (*su*, *gl*, *Tu*) very poor germination of the sugary endosperm seed in this group decreased the stand appreciably. The number of virescent seedlings present in group 5 (*pr*, v_2) was fewer than expected from a normal backcross because many of them died shortly after emergence. The classification into starchy and sugary endosperm in group 6 was good but, due to the inexperience of the writer, there may have been some misclassification of the plants segregating for *Pl* vs. *pl*. They normally show up in b plants as purple vs. reddish anthers, and in B plants

as purple vs. sun red plants. If the r^g allele is present along with b , the two classes cannot be distinguished. A relatively small number of plants was available for the test in group 8 (j, ms_8) because of poor germination. Also, since the male sterile plants produced no pollen, segregation for this character versus pollen sterility could be studied only by classifying the non-male sterile plants. There is a possibility that the yellow vs. white endosperm colour segregation was due to the factor pair Yy located in chromosome 6. If so, this gives further support for the absence of any change in chromosome 6 as the cause of pollen sterility.

As pointed out above, long regions of many of the chromosomes were not covered in the linkage tests, making it impossible to state definitely from these tests that a certain chromosome was not involved in the production of sterility.

The tests which appear to indicate linkage will now be discussed.

Tests for Linkage Group 3— a, ts_4, na

The genes used (a, ts_4, na) are all located in the long arm and entered the cross together. In addition to low viability of seed, in several cases, $na\ ts_4$ plants did not shed any pollen. As none of the tassel seed plants shed pollen readily at any time, at least not until late, some tassel branches may have been collected too early for a satisfactory classification for sterility. The data show a much higher proportion of these was classed as partially sterile than of the ts_4 or Na classes. The P value of 0.02-0.05 for na and for ts_4 appears to indicate linkage between sterility and each of these characters; however, a check of the data shows that the association is not in the direction expected, i.e. it is not between the characters which entered the cross together. This is shown also by a calculation of the recombination value which for ts_4 is 57.0 ± 3.5 and for na is 57.8 ± 4.6 , i.e. above 50 per cent in both cases. Hence there is no good evidence for association of partial sterility with this linkage group.

With r and g in group 10, there were few plants because one cross produced all plants with semi-sterile pollen and was omitted and a second did not segregate for golden plants. Since the two progenies which did segregate for pollen sterility produced more plants of this class than expected from a backcross, and the degree of sterility of many of these was considerably higher than in the other groups, it is probable that some other abnormality was present also; the test was unsatisfactory. Even assuming this is not true, here, again, the parental classes are fewer than the new combinations and the P value of 0.02-0.05 cannot be interpreted to mean association.

Tests with Linkage Group 2— B, gl_2, lg, v_4, Ch

The genes used in this study were well distributed along the entire length of the chromosome as shown in Table 4. The segregation for chocolate (Ch) and colourless pericarp was not obtained in 1946 due to late maturity but was secured in supplementary data collected in 1947.

The summary of results in Table 5 shows P values which indicate linkage of the pollen sterility with each of the genes B, v_4 , and gl_2 , but not for lg or Ch in the same chromosome. Since the P values from X^2 for

TABLE 6.—SUMMARY OF TWO-POINT LINKAGE DATA FOR PARTIAL STERILITY AND GENES IN CHROMOSOME 2, BACKCROSS DATA. THE 304 TOTALS ARE 1946 DATA; THE 166 TOTALS ARE 1947

Genes tested, group 2	Normal pollen		Partially sterile pollen		Total plants	Recombination values $\pm$ S.E.
	X	x	X	x		
<i>B - b</i>	52	89	110	53	304	34.5 ± 2.7
<i>Ch - ch</i>	41	32	39	54	166	42.8 ± 3.8
<i>Gl₂ - gl₂</i>	60	82	90	72	304	43.4 ± 2.8
	29	44	42	51	166	48.2 ± 3.9
Total	89	126	132	123	470	45.1 ± 2.3
<i>Lg - lg</i>	66	76	80	82	304	48.7 ± 2.9
	37	36	58	35	166	43.4 ± 3.8
Total	103	112	138	117	470	46.8 ± 2.3
<i>V₄ - v₄</i>	24	118	139	23	304	15.5 ± 2.1
	12	61	85	8	166	12.0 ± 2.5
Total	36	179	224	31	470	14.3 ± 1.6

heterogeneity for the associations with sterility are higher than the minimum level for significance in all ($P = 0.1$ to 0.2 for *gl₂*, $P = 0.05 - 0.1$ for *B*, $P = 0.3 - 0.5$ for *v₄*), the variations between the different progenies is no greater than expected on the basis of random sampling. These data summarized as 2-point tests are in Table 6. The recombination values between partial sterility and each character are: 15.5 ± 2.1 with virescent seedling - 4 (*v₄*), 34.5 ± 2.7 with plant colour booster (*B*), and 43.4 ± 2.8 with glossy seedling - 2 (*gl₂*). For the *v₄* test, all three progenies show a highly significant and consistent deviation from 50 per cent. For *B* the deviation is significant for all but one progeny, and it is significantly less than 50 per cent on the total population. With *gl₂*, in only one of the three crosses is there a significant deviation from the 50 per cent of recombination. The deviation is slightly larger than $2 \times$ S.E. and therefore significant on the total population.

The data from three crosses are presented in Table 7 as a 5-point linkage test. These data which show the numbers in the different cross-over classes indicate that the gene order is *lg - gl₂ - v₄ - sterility*. This means that the sterility character is located in the long arm distal to the location of *v₄*. The coincidence values have high standard errors and do not deviate significantly from 1.00. Larger populations are needed before drawing any conclusions with regard to interference across the centromere.

Additional data for linkage group 2 were obtained from a segregating population grown in 1947 at University Farm in St. Paul, Minnesota. Unfortunately, the plants were not classified for the colour booster character (*B-b*). The segregation for chocolate and colourless pericarp (*Ch-ch*), as well as for the other characters included previously in this group, was studied. Considerable difficulty was experienced in classifying a number

TABLE 7.—FIVE-POINT LINKAGE TEST, GROUP 2 IN WHICH THE F₁ GENOTYPE, $\frac{++B+sterility}{lg\ g^{\frac{1}{2}}+v_4} +$ WAS BACKCROSSED TO $lg\ g^{\frac{1}{2}}+v_1 +$, 1946 DATA

Parental combinations	Recombinations					
	Region 1	Region 2	Region 3	Region 4	Regions 1 and 2	Regions 1 and 3
57 52 109 35.9 per cent	13 19 32 10.5 per cent	18 21 39 12.8 per cent	23 27 50 16.5 per cent	8 14 22 7.2 per cent	3 1 4 1.3 per cent	4 8 12 4.0 per cent
	Regions 1 and 4	Regions 2 and 3	Regions 2 and 4	Regions 3 and 4	Regions 1, 2, 3	Regions 1, 2, 4
	0 3 1.0 per cent	5 9 3.0 per cent	2 5 1.6 per cent	7 13 4.3 per cent	2 2 0.7 per cent	2 2 0.7 per cent
	Regions 1, 3, 4	Regions 2, 3, 4	Regions 1, 2, 3, 4	Total = 304 Recombination percentages: $lg\ g^{\frac{1}{2}} - 18.4, g^{\frac{1}{2}} B - 20.7,$ $B\ v_4 - 20.0, v_4\ sterility - 15.5$		
	— — —	0 1 1.0 0.3 per cent	1 1 1.0 0.3 per cent			

Coincidence—Regions 1 and 2 c = 0.78 ± 0.22
Regions 2 and 3 c = 0.71 ± 0.16
Regions 3 and 4 c = 1.10 ± 0.22

TABLE 8.—FIVE-POINT LINKAGE TEST, GROUP 2 IN WHICH THE F₁ GENOTYPE $\frac{+}{lg} \frac{+}{gl} \frac{+}{v_4} + \frac{+}{sterility} + \frac{+}{Ch}$ WAS BACKCROSSED TO $lg \ gl \ v_4 + +$, 1947 DATA

Parental combinations	Recombinations				
	Region 1	Region 2	Region 3	Region 4	Regions 1 and 2 Regions 1 and 3
20 19 39 23.4 per cent	5 2 7 4.2 per cent	10 14 24 14.5 per cent	3 3 6 3.6 per cent	14 10 24 14.5 per cent	13 3 16 9.6 per cent
	Regions 1 and 4	Regions 2 and 3	Regions 2 and 4	Regions 3 and 4	Regions 1, 2, 3
	4 3 7 4.2 per cent	0 1 1 0.6 per cent	10 10 20 12.1 per cent	1 3 3 1.8 per cent	0 1 1 0.6 per cent
	Regions 1, 3, 4	Regions 2, 3, 4	Regions 1, 2, 3, 4	Total = 166 Recombination percentages: $lg\ g_2 - 27.7, \ g_2\ v_4 - 47.0,$ v_4 sterility - 12.0, sterility $Ch - 42.8$	
	0 1 1 0.6 per cent	1 2 3 1.8 per cent	3 4 1 2.4 per cent		

Coincidence—Regions 1 and 2 c = 1.39 ± 0.14
Regions 2 and 3 c = 0.96 ± 0.22
Regions 3 and 4 c = 1.29 ± 0.25

of the pollen samples, in spite of their having been collected and preserved in alcohol. The 5-point data are summarized in Table 8. The 2-point data for the four phenotypes involving pollen fertility and each genetic marker are included in Table 6. Inspection of these data in Table 6 reveals no marked deviations which might result if errors in pollen sterility classification were numerous and in one direction. Here also the order is $lg - gl_2 - v_4$ - sterility. The recombination between *Ch* and sterility is 42.8 ± 3.8 the deviation from 50 per cent approaching significance, being only slightly less than $2 \times \text{S.E.}$ The recombination value between *Ch* and v_4 is 41.6 ± 3.8 which is practically the same as that shown in normal stocks (Table 4). The location of *Ch* is discussed later.

DISCUSSION

In this study there is no evidence for any reduction in genetic crossing over in plants heterozygous for inversion 6071. The recombination value of 29 per cent between *B* and v_4 , which is 8 per cent higher than that reported by Emerson *et al.* (10), may or may not have been due to the use of different stocks. The recombination value between v_4 and *Ch* is 41.6 per cent which is practically the same as that for a normal stock, Burnham—unpublished data in Emerson *et al.* (10).

Heterozygous inversions in *Drosophila* reduce the frequency of observed genetic crossing over within the inverted segment and in adjacent regions. Experiments by Sturtevant and Beadle (18) show that they may also reduce cytological crossing over but very much less than the amount indicated by the reduction in genetic crossing over. The explanation is that crossing over occurs in the inverted segment, but most of the crossover chromatids are not recovered. In these experiments, enough crossing over occurs to produce about 16 per cent of pollen abortion, yet genetic crossing over was not measurably reduced.

If *Ch* is in the inverted segment, then 2-strand double crossovers within the pachytene loop, one on each side of this gene, would be required to give recovered recombinations between partial sterility and chocolate pericarp. Partial pollen sterility and *Ch* show 42.8 per cent recombination in this study. If 2-strand doubles occur within the loop, then 4-strand doubles should occur also, and at approximately the same frequency. Four-strand double crossovers within the inversion result in double bridges and two fragments at anaphase I. Since no such figures were seen in the cytological analysis, it appears that double crossing over may be rare in this inversion. Therefore, it seems reasonable to conclude that *Ch* is situated outside the inverted segment and on the side opposite to v_4 , i.e. nearer the end of the long arm. It may be so near the end of the chromosome that it shows very little difference in recombination with v_4 or the sterility resulting from the inversion; or is it possible that the acentric fragment is able to persist into the next generation by passing along with a non-crossover chromatid by the mechanism described by McClintock (14)? This might account for the observed rather free recombination of *Ch* with v_4 and with partial sterility. Genetic studies including genes in the inversion and more genes in the distal segment between *Ch* and the outer break are needed. A cytological study of the crossovers should be made also.

The apparent absence of female sterility in plants heterozygous for this inversion (6071) is an interesting feature. This has been observed before by Smith in barley and by McClintock (unpublished) in maize. Sturtevant and Beadle's explanation (18) for the absence of inviable zygotes as a result of crossovers in an inversion in *Drosophila* is that the anaphase I bridge holds the abnormal chromatids to the centre of the dyad during the second meiotic division, leaving the normal chomatids free to move to the end cells. This may explain the lack of ovule sterility in maize. It is known that there is a linear quartet of megaspores in maize, the chalazal cell of which develops into the female gametophyte. In this study, it was observed that the bridge was broken in many figures before telophase I, and beyond recognition before completion of the cell wall, apparently leaving the chromatids free to proceed to either cell during division II. It is difficult to see how the explanation proposed for *Drosophila* operates here unless the bridge persists longer than this during meiosis in the megasporocyte, or the second division proceeds more rapidly without going into as much of an interphase. McClintock (14) presented evidence of at least part of the anaphase I bridges persisting late in meiosis in microsporogenesis.

The degree of pollen sterility was lower than expected from the proportion of cells observed with bridges and fragments in anaphase I. However, this may have been due to differences in environment since pollen counts were made on field-grown plants and the cytological observations were on greenhouse grown plants. Swanson (19) in his study of inversions in *Tradescantia*, observed that the proportion of cells with bridges increased from 17.5 per cent to 47.8 per cent as the temperature during meiosis was increased from 12° C. to 27° C.

Inversions are widespread in nature, in both plants and animals. Various studies in *Drosophila* have revealed that collections of flies from different areas may differ only by the presence of an inversion in one of the chromosomes. In other words, inversions may be responsible for the appearance of races within a species.

The extensive breeding work in maize has brought to the attention of corn breeders and geneticists a large number of abnormal characters which had been carried in a hidden condition in the highly heterozygous open-pollinated varieties. Many of these characters are probably due to point mutations, but structural changes in the chromosomes may also be involved. On a few occasions, inbred lines have been found to be carrying interchanges which did not show up until crosses were made with a normal line. An inversion which causes no female sterility, as in the case of 6071, may not be detected. Actually, it may be of limited significance if the single cross of which it is one parent produces ample pollen when used as a male parent to produce double cross seed. However, crossing over in a long inversion may occur in 100 per cent of the cells resulting in close to 50 per cent of sterile pollen; or still more if other chromosomes contain inversions.

Possible uses of inversions in maize breeding problems have been discussed by Dobzhansky and Rhoades (9) and Sprague (16, 17). Dobzhansky and Rhoades have suggested using inversions to determine the yield genes carried on the various chromosomes of the different inbred

lines. A homozygous inversion stock, with some suitable marker in the inverted segment, is crossed with an inbred line and the F_1 backcrossed to the inversion stock. The backcrossed progeny will consist of two types of plants, homozygous and heterozygous for the inversion. Presumably these two classes of plants differ only for the gene differences within the chromosome section marked by the inversion. As gametes resulting from crossing over within the inverted segment are mostly aborted, this provides a measure of the net effect of all dominant or partially dominant genes within this segment.

Sprague (16,17) has presented data on use of the inversion method indicating that it is feasible. A fifth chromosome inversion stock was used in which the inverted segment involved about 0.3 of the chromosome and was marked by the *pr* (red aleurone) colour factor. This was crossed with an inbred line (*Pr*) purple, backcrossed to the inversion stock (*pr*), and the homozygous and heterozygous classes were compared for several characteristics. It was found that differences in yield per plot and weight per 500 kernels were significant. In each case the dominant factors were contributed by the dent corn inbred.

Sturtevant and Beadle (18) have discussed crossing over in included inversions in which a single crossover may give rise to a gamete which has a duplication for one or two genes but is otherwise normal. In plants as well as in *Drosophila* a gamete of this type may function in the production of a viable zygote. In plants, there is a possibility that such a duplication might be established in homozygous condition to increase the dosage of certain desirable genes, e.g. disease resistance or genes for sugary or other characters.

The use of structural changes such as translocations and inversions for breeding purposes is still in the experimental stages. Further investigations should give more detailed information on the possibilities of their uses. As more genes are located on the various chromosomes it will become easier to determine the breakage points of an inversion or other structural changes, and increase their usability by introducing marker genes.

SUMMARY

1. A cytogenetic study of a line of maize showing low pollen sterility but normally filled ears is described.

2. Cytological studies showed single bridges and fragments but no double bridges at anaphase I. There was a smaller number of cells with irregularities in division II. No bridges were observed at division II. Pachytene observations revealed the presence of loops, asynapsis, and reverse pairing in chromosome 2, similar to those expected from an inversion. One of the breaks was located at about 0.1 of the distance from the centromere to the end of the long arm, and the second break at about 0.6 of the long arm, near the pycnotic knob which is not included in the inversion. The total length of the inverted piece appears to have been about 50 per cent of the long arm.

3. The low pollen sterility due to the inversion was transmitted through both male and female. Progenies of crosses between normal and partially sterile plants varied rather widely in the proportions of low sterile plants,

the total for all the segregations being 49.3 per cent. The degree of pollen sterility varied from 12 to 22 per cent in different plants, but the average was 16.5 per cent.

4. A 5-point linkage test between genes in chromosome 2 and the low pollen sterility character associated with the heterozygous inversion indicated the order $lg - gl_2 B - v_4 - \text{sterility}$. Between v_4 and sterility the recombination value was 14.3 per cent. The recombination between sterility and colour booster (B) on the same chromosome but in the short arm was 34.5 per cent whereas between v_4 and B it was 29.0 per cent. A second 5-point test including Ch but not B gave 42.8 per cent recombination between sterility and Ch and 41.6 between v_4 and Ch . The gene, Ch , is probably located in the long arm of chromosome 2 distal to the inversion.

5. No reduction in genetic crossing over was observed in the inversion heterozygote, but the regions involved may have been too long.

6. It is suggested that eventually inversions may be of use in the production of stocks carrying a duplication for desirable genes.

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OBSERVATIONS ON SIX YEARS' SEED TREATMENT OF SOYBEANS IN ONTARIO¹

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Until 1940 the average annual acreage of soybeans in Canada did not exceed 10,000 acres (2). By 1944, however, soybeans were grown in the Dominion to the extent of 45,000 acres (8) of which 44,700, yielding 845,000 bu. valued at \$1,690,000, were grown in the Province of Ontario. Production in 1948 from a total of 94,000 acres (9) reached 1,683,000 bu. with a market value close to \$4,000,000. Most of the soybean production in 1948, as in preceding years, was in southwestern Ontario.

During the period of rapidly-expanding acreage from 1942 until 1948, 14 parasitic diseases were reported by the present authors (5, 6) as occurring on soybeans in the high-production area of southwestern Ontario. Included among these were several that have been regarded by workers elsewhere as constituting a serious menace to the crop (7, 1). As a phase of the pathological investigations that have been carried out at Harrow in an endeavour to keep abreast of the potentially dangerous disease situation, a seed-treatment project, inaugurated in 1943, has been continued during the past six years. Originally, the experiment had been projected on a ten-year basis, but since the results indicate that little is to be gained by further repetition of the tests, the project has now been discontinued. A review of the investigations is presented in the present paper.

MATERIALS AND METHODS

Seed of A. K. Harrow, the variety best adapted to and, until recently, most extensively grown in the district, was used in all the tests. Each year an attempt was made to procure seed of as poor quality as possible, i.e., seed low in viability and high in disease potentiality. In some instances, such seed was readily available. For example, in 1942, due to extremely unfavourable weather conditions, soybean seed produced in southwestern Ontario was the poorest for many years. A sample selected for the 1943 spring trials showed a germinating capacity of only 23.4 per cent and a visibly diseased fraction of 40 per cent. In 1946, by examining seed lots from a number of different sources, it was possible to compound a sample containing 21 per cent definitely diseased seed, viz. 7 per cent mildew-encrusted (*Peronospora manshurica* (Naoumoff) Sydow), and 14 per cent "hilum canker", a condition characterized by a more or less distinct brownish-discoloured, canker-like injury immediately surrounding the hilum. The seed selected for the 1948 tests contained mildew-encrusted seed to the extent of 20.5 per cent. In 1944, 1945 and 1947, seed showing only a trace of disease had to be used.

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The protectants used, together with their composition and source, were as follows:

Spergon: tetrachloro para benzoquinone; Naugatuck Chemicals, Division of Dominion Rubber Company, Ltd., Elmira, Ontario.

Fermate: ferric dimethyldithiocarbamate, 70 per cent active material, wettable; Canadian Industries Limited, Chatham, Ontario.

Arasan: tetramethyl thiuramdisulphide, 50 per cent active material, non-wettable; Canadian Industries Limited, Chatham, Ontario.

Phygon: (later replaced by Phygon-XL): 2,3-dichloro-1,4 naphthoquinone; Naugatuck Chemicals, Division of Dominion Rubber Company, Ltd., Elmira, Ontario.

F-800: 2,4,5-trichloro phenyl chloroacetate; Dow Chemical Co., Midland, Michigan.

Seed lots after being treated early in February each year, at the rates indicated in Table 1, were packaged and stored in the laboratory until planting-time in May.

To promote natural infestation of the soil, the tests were carried out season after season in the same location. Each year, prior to planting, the soil, a Fox sandy loam, received an application of a 2-12-10 commercial fertilizer applied broadcast at the rate of 250 lb. per acre. All planting was done by hand in a randomized, 5-replicate design, the test unit within each plot comprising duplicate rows, 35 ft. long in 1943, 30 ft. from 1944 to 1948, inclusive. The rows, spaced 30 in. apart, were planted at the rate of 35 lb. per acre in 1943, and 30 lb. subsequently, the latter rate having been found by test to give maximum yield for the type of soil on which the experiment was being conducted. Planting dates were as follows: May 18 (1943); 15 (1944); 24 (1945); 13 (1946); 23 (1947), and 20 (1948).

Each year, counts made three weeks after planting furnished the data on emergence. Except for hand-weeding, cultural treatment of the plots conformed closely with accepted field practice for the crop. In harvesting, the plants were cut near the base of the stem with pruning shears, assembled in bundles, and threshed* the same day. All weighings were made immediately after threshing.

EXPERIMENTAL RESULTS

The results of the six years' experiments, in so far as emergence and yield are concerned, are summarized in Table 1. In regard to statistical treatment of data, the least significant difference between treatment means was determined for yield each year by the method of analysis of variance.

The results as shown in Table 1 are especially interesting for the first year's test in which 40 per cent diseased 1942 seed was used. In that particular test, treatment with Spergon resulted in an increase in yield that was highly significant over that resulting either from non-treated seed

* 1943-1945, J. L. Jones, No. 4, pea and bean thresher; 1946-1948, portable, power-driven, rod-row thresher.

or from treatment with Arasan or with Fermate. In none of the other five tests, however, were comparable results obtained. Even in the case of the 1947 and 1948 seed, diseased to the extent of at least 20 per cent, yield differences between treatments were not significant and only in few instances did treatment give a possible significant increase in yield, e.g., Fermate over check in 1945. The average yields for treatments and check over the 5-year period 1944-1948 are surprisingly uniform.

More noteworthy than the yield differences between treatments or between treatments and check in any given year (except 1943) are those between different years. In the 1947 test, for example, yields were lower than for corresponding treatments in any other year. The reason for these lower yields is not difficult to explain. The mid- and later-summer season of 1947 was marked by a period of severe drought and high temperature, during which the experimental plots were extremely heavily infested by a species of red spider. The effects of the latter, superimposed upon those resulting from drought, undoubtedly were responsible for the reduced yields. Not so readily explainable, at first glance, however, are the tremendously increased yields in 1948, especially in view of the fact that, that year, fertilizer application was identical with and cultural treatments were similar to those of preceding seasons. Moreover, the increased yield cannot be explained on the basis of a difference in viability in favour of the seed used in 1948. Indeed, as Table 1 shows, emergence in 1948 was from 2 to 9 per cent lower than that in 1947. In a general way, it was known that the "weather" had been much more favourable for soybeans in 1948 than in certain, at least, of the preceding years. This circumstance emphasized the importance in such studies as these of careful consideration of "weather" in relation to other factors affecting emergence and yield. With this in mind, each year, for the period commencing May 10 and ending August 31, maximum and minimum daily temperatures, as well as rainfall, were plotted and expressed graphically as shown in Figure 1. Average seasonal yield for each treatment and check is also shown in the same figure.

Referring to Table 1, it will be noted that emergence in 1945 was generally lower than for any other year except 1943 when the extremely poor seed had been used. The planting date in 1945 was May 24. For an 11-day period just prior to that date, the minimum daily temperature ranged from 33° to 45° F., with an average of about 39° F. Then, following planting, for a 10-day period from May 29 until June 8, the minimum daily temperature again was low with an average of about 40° F. In no other year was the seed planted under such cold weather conditions. Since soil moisture was not lacking, the evidence strongly suggests that temperature was an important factor modifying emergence in 1945. Emergence for treated seed, it will be noted, averaged about 79 per cent, whereas that for untreated seed was 62.8 per cent. The increase of 16.2 per cent in favour of the treated seed would support the following statement made by Porter (10) in 1946: "Given unfavourable conditions for germination in the field, one could expect seed protectants to be of value even with seed of high vitality and if seed of low vitality were used the benefit should be greater." Unfortunately, increased emergence does not necessarily mean increased yields. This is clearly shown if emergence and yields for 1945 are compared

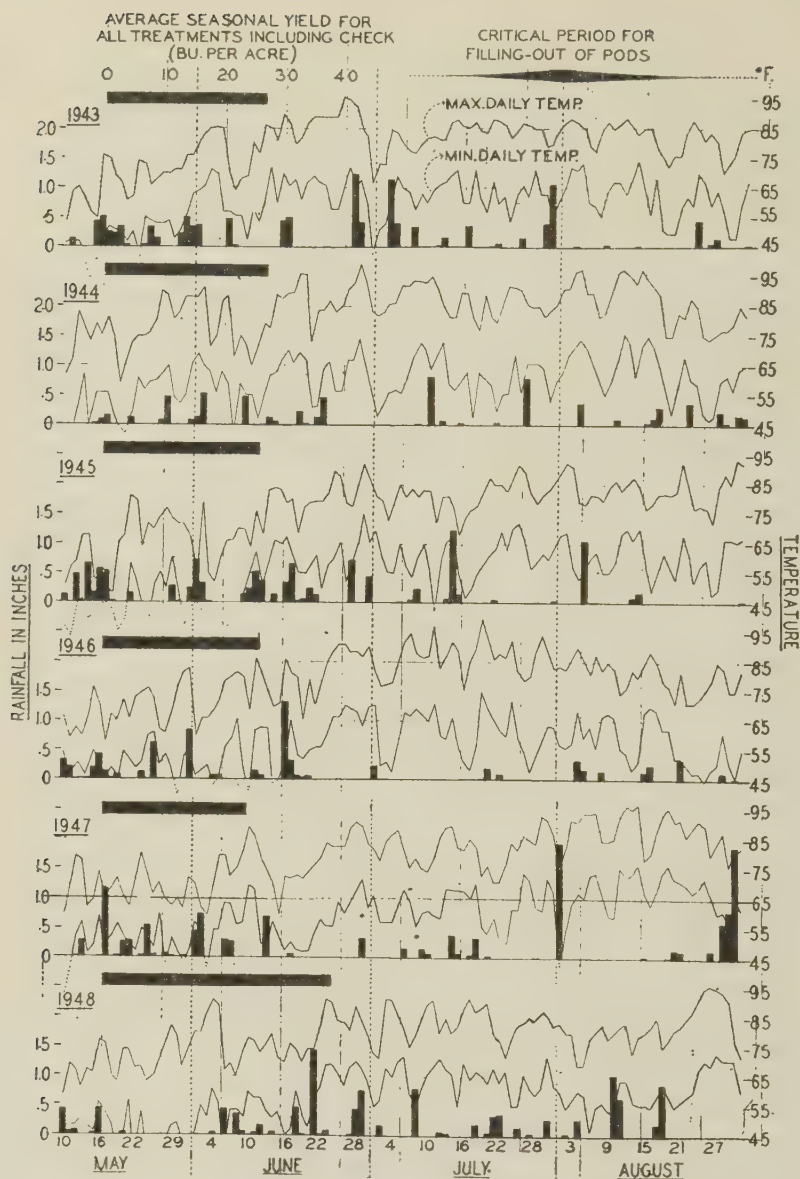


FIGURE 1. Seasonal rainfall and temperature in relation to yield of soybeans in experimental plots for the 6-year period 1943 to 1948, inclusive.

with those of 1944 and 1946. The question of the lack of correlation between emergence and yield has been discussed at length in a previous publication (5) and need not be dealt with further here. The point would seem to be established, however, that weather can be a factor in modifying yield even in the case of treated seed.

Later in the summer, when the pods are filling out, the weather is probably a more critical factor, as far as yield is concerned, than it is in the early growing season. In the Harrow area, the important period for pod

and seed development extends from early in July until late in August. In examining the temperature conditions that prevailed during the 57-day period July 5 until August 31, for the different years of the test, it was found that the maximum temperature exceeded 85° F., on 21 days in 1943; 33 in 1944; 17 in 1945; 27 in 1946; 28 in 1947, and 16 in 1948. By this criterion it may be adjudged that, relatively, the mid-summer periods of 1944, 1946 and 1947 were hot; those of 1945 and 1948 appreciably cooler; while that of 1943 displayed a temperature intermediate between the extremes of the other years. If temperature were the chief limiting factor modifying yield, then it might be expected that yield difference could be correlated with temperature differences such as those just indicated. No such correlation exists, however, and temperature per se is ruled out as the important factor modifying yield. Of the remaining factors, soil moisture would present itself as the most important. During the period in question, i.e., July 5 until August 31, total precipitation for the different years was as follows: 1943, 3.33 in.; 1944, 3.68 in.; 1945, 3.24 in.; 1946, 1.84 in.; 1947, 6.97 in., and 1948, 4.52 in. If there were a direct correlation between amount of rainfall and yield, then yield should have been highest in 1947, intermediate in 1948, and lowest in 1946. No such gradation occurred, however, and it is obvious that, if a correlation between precipitation and yield does exist, it cannot be established by a consideration only of amount of rainfall. Distribution presents itself as a factor that must be taken into account. When Figure 1 is examined, it will be noted that, in 1948, for the 57-day period in question—and, in fact, for most of the growing season—rainfall was not only so adequate but was also so evenly distributed that a soil even as porous as the Fox sandy loam, on which the tests were being carried out, never approached the point of dryness at which growth of the soybeans might be adversely affected. Such was not the case, however, even in 1947 when, between July 5 and August 31, the rainfall of 6.97 in. exceeded by 2.45 in. that of 1948 (4.52 in.), for the same period. In 1947, as Figure 1 shows, most of the 6.97 in. came in almost cloud-burst proportions on August 1 and on August 30. Preceding August 1 and from that date until August 30, the weather was hot and dry, the soil dried out and for appreciably long periods the soybean plants showed severe wilting. In 1948, as has been pointed out above, the showers that produced 4.52 in. of rain, between July 5 and August 31, were ideally spaced and the plants never lacked adequate moisture. When additional comparisons are made between the rainfall of 1948 and that of 1944, 1945 and 1946, the importance of distribution of precipitation as a factor modifying yield becomes increasingly evident.

DISCUSSION

In 1947, in reporting the results of soybean seed treatment investigations up to that time, the present authors (5) stated that, "With poor quality, weather-damaged seed . . . and with the cracked-coat fraction of an otherwise high-quality seed . . . treatment with Sperguson increased emergence and yield. These were the only instances, however, in which increases in early stands of plants as the result of seed treatment were correlated with statistically significant increases in yield." It was further pointed out that these results were substantially in accord with those

reported by several contemporary workers in the United States, all of whom had found that, although seed treatment (not necessarily with Spergon in all cases) might give increased stands over non-treated checks, yields in general remained unaffected. As the result of more recent work as reported not only here by the present authors but also by investigators in the United States (3, 4, 11), there would seem to be no reason for modifying the earlier view that if high-germination, good quality soybean seed is planted, seed treatment is of doubtful value.

SUMMARY

From 1943 to 1948, inclusive, soybean seed of the variety A. K. Harrow, varying from year to year both as to germinability and disease potentiality, was treated with Spergon, Arasan, Fermate, Phygon, Phygon-XL and F-800 and planted in outdoor plots in a randomized, 5-replicate design. In the case of the extremely poor-quality 1943 seed (germinating capacity 23.4 per cent and visibly diseased to the extent of 40 per cent), treatment with Spergon increased emergence and yield. This was the only instance, however, in which an increase in early stand of plants, as the result of seed treatment, was correlated with a statistically significant increase in yield.

More noteworthy than the effect of seed treatment in modifying yield was that of favourable weather, a remarkable increase of some 10 bu. per acre in 1948 over all other years, apparently being correlated more closely with an adequate, well-distributed rainfall than with any other factor.

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ROLLER CRUSHER FOR DRYING HAY

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Means of suitably curing or drying forage crops is a major problem in farm operation. Numerous methods and various types of equipment have been used in an attempt to protect the hay crop from the weather and to decrease the length of time that this crop normally remains in the field during curing and harvesting operations. The crushing of green hay by a machine consisting primarily of two steel rollers is one device which has been used in an endeavour to increase the rate of drying or curing hay. To determine the value of this machine in haying operations, experiments have been conducted at the Central Experimental Farm, Ottawa, in which the rate of drying of crushed hay was compared with uncrushed hay.

The crusher used in the tests consists of two steel rollers, six inches in diameter and five feet long, a pick-up device for lifting the hay into the rollers, and an auxiliary engine for driving the rollers. Two springs are used to maintain a pressure between the rolls and the speed of the rolls is approximately 250 revolutions per minute.

In principle, the machine is designed to sufficiently compress a swath of hay as it passes between the rolls to crack the stems of plants and to bruise the leaves. It is not designed to squeeze or press moisture out of

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FIGURE 1. Front view of crusher



FIGURE 2. Rear view of crusher

the plants as might be expected; but there is some free moisture present on the compressed hay due to bruising of both the stem and leaf. The action of the machine is intended to increase the rate of drying of the stems of the plants in order that the stem might dry at approximately the same rate as the leaf.

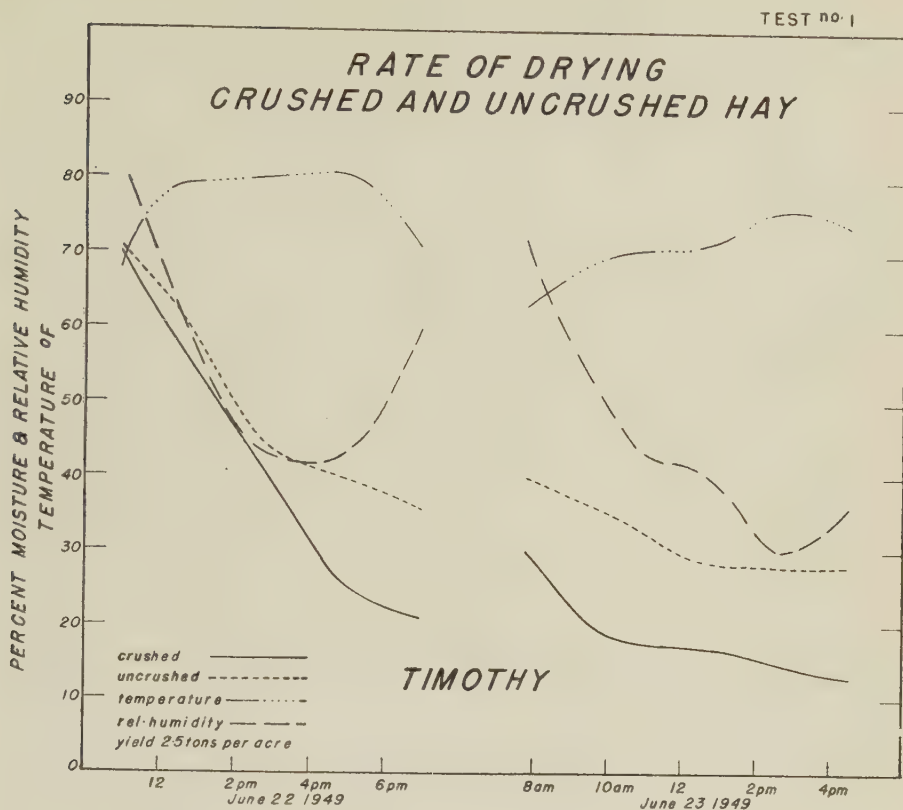
Field units for the crushing of hay did not originate recently; some units were built prior to 1937, and the idea may have been conceived many years earlier. However, the mechanism of the first machines was not well developed and they were not produced or available in any quantity for farm use.

EXPERIMENTS ON CRUSHED AND UNCRUSHED HAY

Field tests were conducted on hay crops consisting of first cut timothy, alfalfa and clover (3 to 2), alfalfa and timothy (3 to 1) and second-cut clover. Every other swath in the field was crushed while the intermediate swaths served as a check. Replicate samples of hay were taken to determine the rate of drying of the crushed and uncrushed material. Other data, including temperature and relative humidity, were noted and plotted on the attached charts. All tests were performed when the weather was favourable for curing hay.

Test No. 1

This test was conducted on a crop of timothy that was cut approximately two days before full bloom and which yielded 2.5 tons per acre. The crop was cut at 8.30 a.m. and the moisture content of the crop was

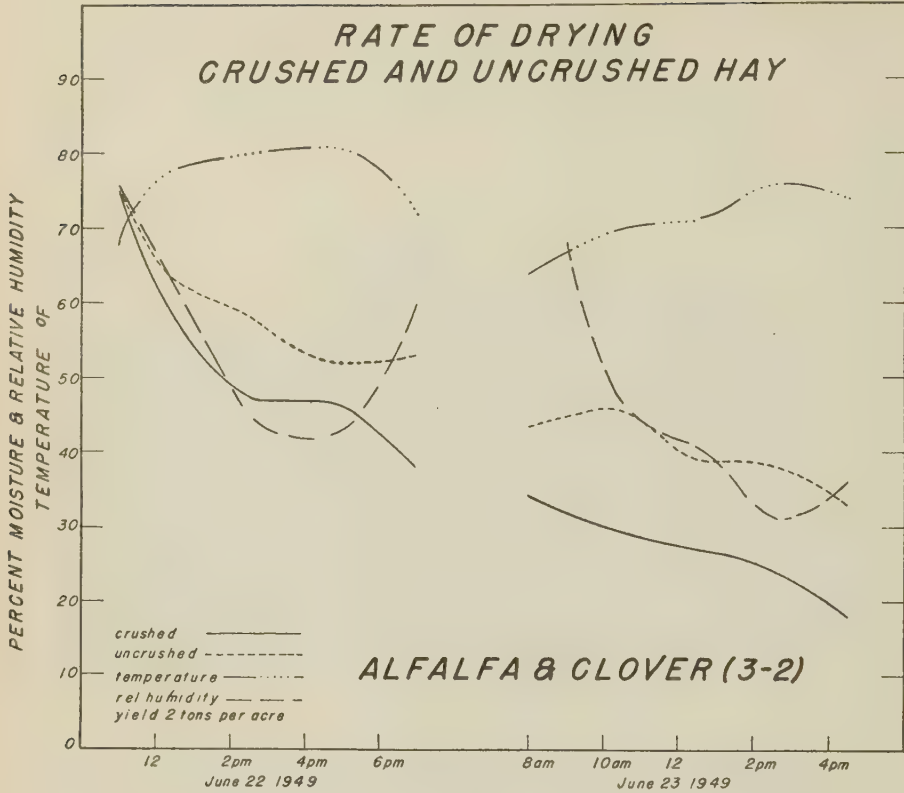


70 per cent when it was crushed at 11 a.m. From the first graph it may be noted that the crushed material reached 25 per cent moisture at 5 p.m. in the afternoon and could have been hauled to storage at this time while the uncrushed material reached a moisture content of only 45 per cent. Both the crushed and uncrushed material gathered moisture during the night.

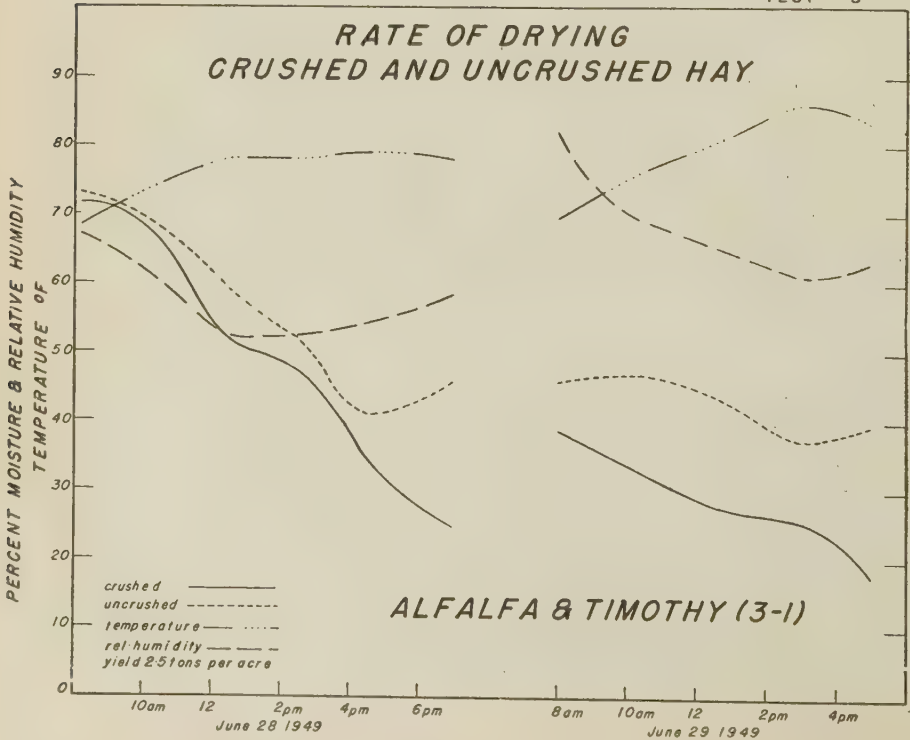
At 9 a.m. of the second day the crushed material was at 25 per cent or 11 per cent lower than the uncrushed material, and thus again suitable for storage. The hay in the field was raked at 3 p.m. and the uncrushed crop was suitable for storage at approximately 11 a.m. of the third day.

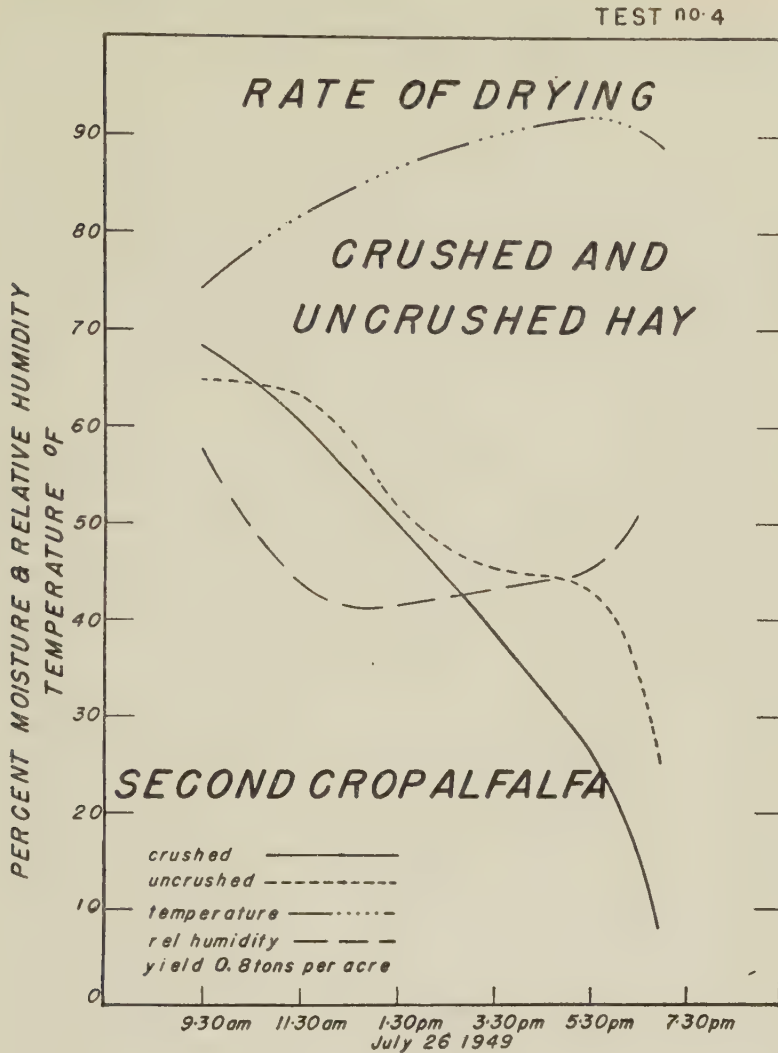
Test No. 2

In this test the crop used was a mixture of alfalfa and clover (3 to 2) that yielded two tons per acre and which was cut at full bloom. On the day the crop was cut the initial moisture was 75 per cent. By 7 p.m. oven-dried samples indicated a moisture content of 54 per cent for uncrushed material and 36.5 per cent for the crushed hay. At 2 p.m. the following day the crushed alfalfa and clover was below 25 per cent and suitable for storage while the uncrushed hay had reached a moisture of 33 per cent. An upward trend in the moisture content curve for uncrushed hay between 5 p.m. and 7 p.m. on June 22 has been attributed to difficulties in obtaining representative samples of the hay as it cured in the swath.



TEST no-3





Test No. 3

The crop used for field test No. 3 was an alfalfa timothy mixture (3 to 1) with the alfalfa at three-quarter bloom and the timothy at full bloom. This crop yielded 2.5 tons per acre. The graph for alfalfa and timothy shows that the crushed hay was sufficiently dry for storage at 7 p.m. on the day it was cut, while the other material contained 45 per cent moisture. As the crushed hay could not be hauled from the field that evening, it gathered moisture during the night and was not stored until after noon on the following day, while the uncrushed hay could not be placed in the barn until one day later. In this test the uncrushed material did not show any increase in moisture content during the night. As both crushed and uncrushed hay normally gather moisture overnight this apparent discrepancy could only be attributed to a sampling error. Even

by taking a considerable number of samples of hay as it cures in the field, and by attempting to secure representative samples, discrepancies of this nature were not entirely eliminated.

Test No. 4

Second-cut alfalfa yielding 0.8 tons per acre was used in the final test. Due to the dry season this crop was poor with the plant height ranging from 4 to 14 inches. The initial moisture content was below the other crops tested. The crushed alfalfa dropped to a moisture content of 25 per cent by 5.30 p.m., and the uncrushed reached this moisture content at 7 o'clock of the same evening. Due to this light yield, high temperatures, low relative humidity and good air circulation there was very little difference between the crushed and uncrushed samples. On the second day both samples were below 20 per cent moisture content; therefore, testing was discontinued.

SUMMARY

In the three tests on first-cut crops of hay the crusher operated in a fully satisfactory manner. On the second-cut crop, which was short and particularly low in yield, a considerable amount of difficulty was experienced with the machine. Even though the speed of travel was varied from three to five miles per hour, the pressure on the rolls was varied, and other adjustments made, it was not possible to obtain an even flow of the material through the crusher rolls.

The tests indicate that there is a closer relationship between the rate of drying and air humidity for uncrushed than for crushed hay. It may be noted from the graphs that uncrushed or ordinary hay started to absorb moisture sooner than the crushed hay when the humidity began to increase during the late afternoon and evening.

In general, it appears that crushing of the hay is beneficial for early cut hay, which has a reasonably high yield and which contains a considerable amount of moisture at the time of cutting. Three tests show that during favourable weather crushed hay cut in the morning was suitable for storage by the evening of the same day, and that this hay could be conveniently stored at noon on the following day. Uncrushed hay required two days to cure under the same conditions and could only be hauled to storage at noon on the third day. This represents a saving of time of one day in three days under favourable weather conditions.

According to experiments conducted by Jones (1), the crushed method proved more beneficial on crops or plants having thick heavy succulent stems and leaves than on other crops. In the above tests there was no significant difference between timothy and alfalfa clover mixtures. Feeding tests were not conducted on the crushed and uncrushed hay at Ottawa, but Pennsylvania State College (2) reports no significant difference in the feeding value of the hay which has been crushed and hay that is cured in the regular manner.

In studying the data presented for this experiment it should be noted that results are based only on tests in 1949 when the weather was favourable for curing hay.

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PRELIMINARY STUDIES ON A PYTHIUM ROOTROT OF SPANISH ONION SEEDLINGS¹

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INTRODUCTION

In recent years a serious rootrot of Spanish onion seedlings has been observed in numerous greenhouses in southwestern Ontario. Because of the yellowish discoloration of the leaves of affected seedlings and of the occurrence of the latter in scattered groups in the flats, in which they are commonly grown, the trouble has come to be known locally as "Yellow Patch".

The disease has been severe whether the seed has been planted in steamed or in non-steamed soil. Although the number of seedlings affected varies from flat to flat in any given planting, the trouble develops in a high percentage of flats in every greenhouse previous to the transplanting of the onions to the field. By mid-April, at the usual time for transplanting, seedlings are often so stunted and unthrifty, as a result of extensive root injury, that frequently less than 50 per cent are large enough to be set in the field. Because of the consistent occurrence of this trouble it ranks in economic importance as the most serious seedling disease of Spanish onions in southern Ontario. The purpose of this preliminary paper is to report the cause of the disease.

LITERATURE REVIEW

No extensive investigations of rootrot of Spanish onion seedlings appear to have been conducted hitherto. In 1948, however, Semeniuk (3) briefly mentioned a *Pythium* seedling rot and root necrosis of *Allium cepa*. By plating diseased roots on agar, the investigator consistently obtained a high percentage of *Pythium* species, including *P. irregulare*, *P. ultimum*, *P. spinosum*, *P. mamillatum*, *P. debaryanum* and *P. graminicolum*. He also found *Fusarium* developing from nearly every root and less frequently *Phoma terrestris*, a chlamydosporous *Phoma* sp., and other fungi. According to this author, symptoms of *Pythium* parasitism are seed rotting, pre-emergence seedling rot, stunted emerged seedlings, which often die, seedling damping-off, and lead-coloured or faintly brown, yellowish or pink roots lacking cortex in advanced stages of disease.

DESCRIPTION OF THE DISEASE

The presence of the disease is first noticed about 4 to 7 weeks after seeding and becomes increasingly apparent after the seedlings have been "topped" two or three times. While all the plants in a flat are occasionally attacked, more often, in the incipient stages at least, as the name "Yellow Patch" implies, only part of a flat is affected.

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The conspicuous symptoms are wilting accompanied by yellowing of the tips of the younger leaves and complete blanching and ultimately death of the older leaves. Affected seedlings are severely stunted and exhibit characteristic symptoms of starvation and drought.

Observations in commercial greenhouses indicate that seedlings attacked after they are four or more weeks old are seldom killed outright. Ordinarily, when conditions favour good growth, late-infected seedlings have been observed to recover if left in the original flats for two to three weeks after the usual transplanting time. However, since late plantings result in greatly reduced yields, such recovered plants are of little value.

When diseased plants are carefully pulled from the soil and washed in water, many of the oldest roots are observed to be severely decayed and often only a few fragments of root tissue remain attached to the base of the bulb (Figure 1). Characteristically, the root system manifests an advanced stage of necrosis before above-ground symptoms are very conspicuous (Figures 8 and 9). Concurrent with the rotting of the oldest roots is a tendency for the plant to "bulb" (Figure 1) and to produce new adventitious roots. Plants six or more weeks old have often furnished evidence of having lost roots continuously and yet have continued to produce new roots. The epidermal tissue of the bulbous part of affected onions is frequently brown and necrotic.

When affected roots are immersed in water they are found to be glassy and transparent in appearance. In incipient lesions, however, it has been observed that the vascular cylinder remains as a white strand for some time after the cortical cells have become completely transparent. Furthermore, this sleeve of necrotic, colourless, cortical tissue can be readily pulled from the root with dissecting needles. Older roots, when attacked, become yellow or faintly brown in colour before they collapse. In general, root necrosis develops rapidly.

Microscopic examination of necrotic roots consistently revealed the presence of oospores throughout the root (Figure 2), indicating the invasion of all tissues. The epidermal tissue of the bulb is also invaded by the fungus. Oospores may occur singly or may be aggregated in a cell. In the advancing margin of the lesion both fungus mycelium and sporangia are readily observed. In addition, nematodes are found to be frequent invaders of necrotic roots.

ISOLATIONS FROM DISEASED ROOTS

During the course of the investigation more than 300 root fragments of diseased onion seedlings obtained from several greenhouses were plated on potato dextrose agar. In a high percentage of the earlier isolations, in which diseased tissue, after being surface-sterilized in 1/1000 mercuric chloride solution, was plated on acidified agar, the following organisms were obtained: *Fusarium* sp., *Mucor* sp., *Penicillium* sp., and *Rhizoctonia Solani*. In 90 per cent of the later isolations in which surface sterilization was not used and in which the root fragments, after having been thoroughly rinsed in several transfers of sterile water, were buried in non-acidified agar, a *Pythium* sp. was obtained. Because of the consistency of occurrence of the last-mentioned fungus it was tested for pathogenicity and cultured for identification.

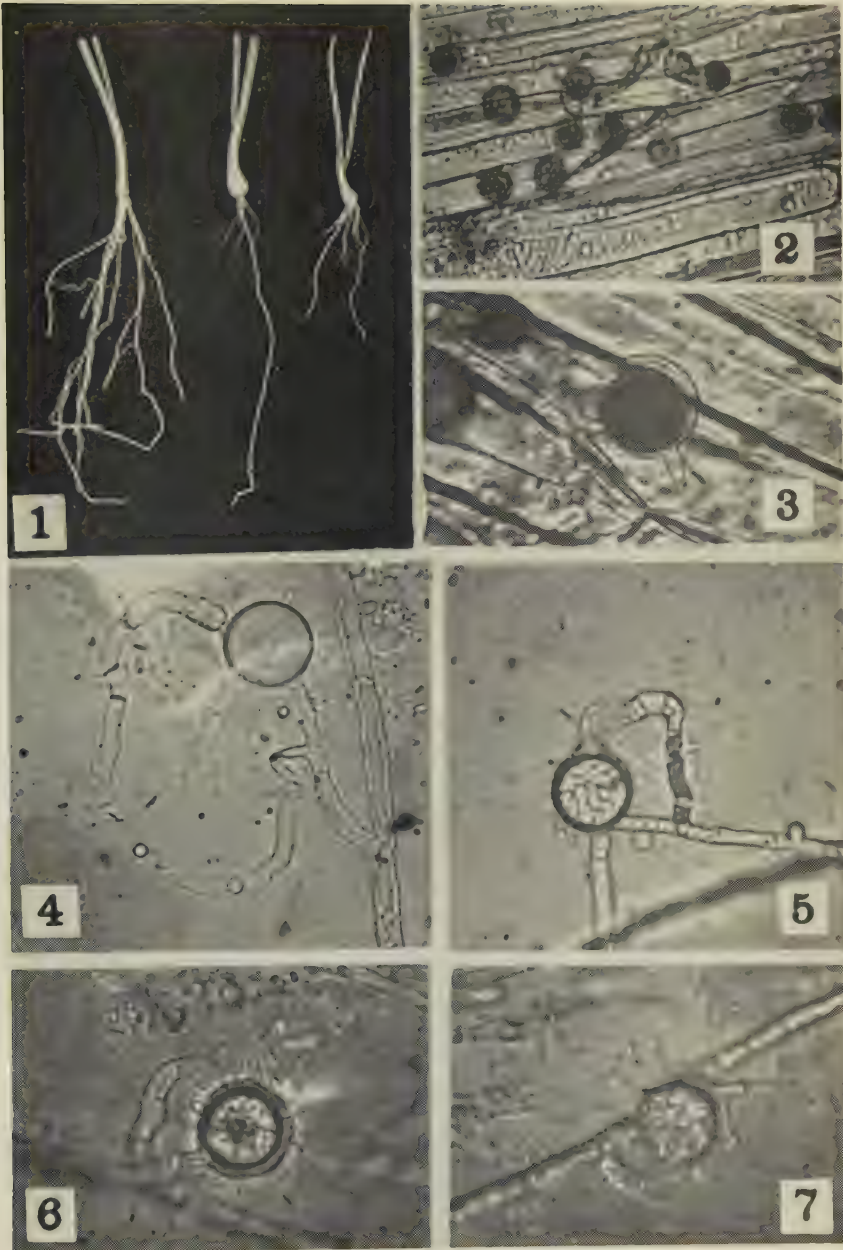


FIGURE 1. Healthy seedling at left with two diseased seedlings at right. Note tendency to bulb in diseased plants.

FIGURE 2. Oospores of *Pythium irregulare* in cortical cells of onion root (X350).

FIGURE 3. Oogonium in necrotic root showing protuberance on oogonial wall (X760).

FIGURE 4. Sexual organs just prior to fertilization. Note the long oogonial projection and the long falcate antheridial branch (X760).

FIGURE 5. Sexual organs just after fertilization (X760).

FIGURES 6 and 7. Stages of sexual reproduction. Note the short oogonial projections in Figure 6 and the longer septate one in Figure 7 (X760).

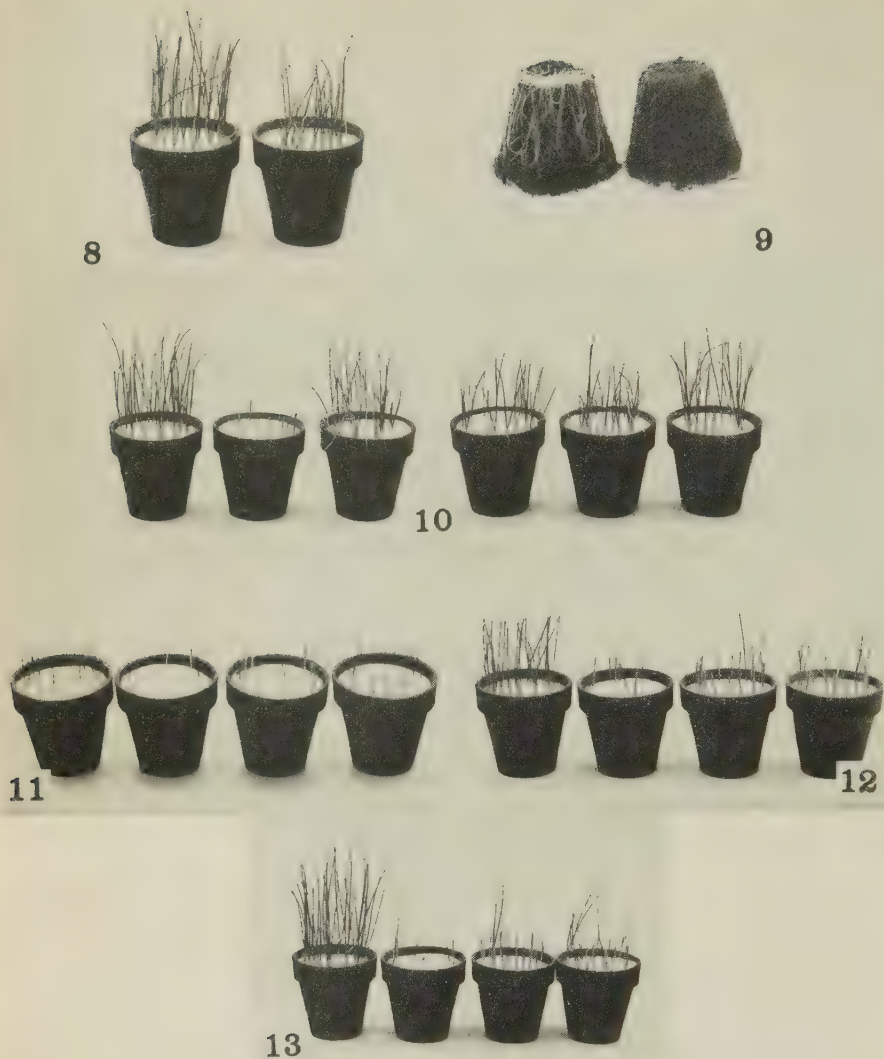


FIGURE 8. Six-week-old Spanish onion seedlings; non-inoculated control at left, seedlings in pot at right were inoculated with *P. irregulare* 17 days previously.

FIGURE 9. The inverted contents of two pots shown in Figure 8. Note the white mass of roots in check at left and scarcely visible, necrotic roots of inoculated seedlings at right.

FIGURE 10. Six-week-old onion seedlings inoculated at different ages with *P. irregulare*. Left to right are check, inoculated at planting, at emergence, at 7, 14, and 21 days after emergence. Toothpicks represent killed seedlings.

FIGURE 11. Sixteen-day-old onion seedlings grown in steam sterilized soil where *P. irregulare* was placed at various levels below the seed. Left to right, check, inoculum placed $\frac{1}{4}$, $1\frac{1}{2}$, and 3 inches below seed. Toothpicks represent killed seedlings.

FIGURES 12 and 13. Same as Figure 11 showing seedlings at 4 and $5\frac{1}{2}$ weeks old, respectively.

PATHOGENICITY

A preliminary test was conducted in the greenhouse in mid-July by infecting steamed soil in which the onion seedlings were growing with agar cultures of the *Pythium* isolate. The fungus was observed to invade the roots of the young seedlings and to cause some necrosis. Attacked plants, however, continued to grow rapidly and manifested no conspicuous above-ground symptoms. In further tests in which the fungus was introduced into vials of nutrient solution where 17-day old seedlings were being grown, the roots were observed to be invaded immediately. All root tissues were then extensively parasitized and the seedlings were killed in a few days.

IDENTIFICATION AND DESCRIPTION OF THE PATHOGEN

When the fungus was grown on potato dextrose agar, sporangia were observed to develop in four to five days and sexual organs (Figures 4, 5, 6, and 7) in five to seven days. In gross morphology and in measurements of size of sporangia, oogonia, and oospores the fungus was indistinguishable from *Pythium irregulare* Buisman as described by Middleton (2).

The sporangia show great diversity in shape, manifesting spherical, elliptical and pyriform types. Spherical to lemon-shaped oogonia are usually intercalary and often possess protuberances that are readily found when the fungus is grown on potato dextrose agar but are only rarely seen in necrotic root tissue (Figure 3). When a small piece of agar upon which the fungus was growing actively was transferred to sterile water in a Petri plate, the nature of the oogonial protuberances could be very clearly seen as further growth was made. The projections are few to numerous, of irregular length and are also irregularly located on the oogonial wall. Long projections are occasionally found to be septate (Figure 7). Antheridia are usually monoclinal, occasionally dichlinal, rarely more than three per oogonium and more often one or two. Considerable variation was found both in the length and shape of the antheridial branch. The antheridial cell is typically short, slightly swollen, crook-necked and borne on a slightly curved stalk (Figures 5, 6, and 7). Occasionally, however, the antheridial cell is long, allantoid-clavate and is borne on a relatively long, sometimes 100 μ , falcate stalk (Figure 4). The oospores are aplerotic. Germination was not observed.

INFECTION EXPERIMENTS

In order to study the pathogenicity of the fungus under conditions of growth similar to those existing in commercial plantings two experiments were conducted in the greenhouse in early spring.

Effect of Pythium Irregulare Upon Spanish Onion Seedlings When Placed at Three Different Depths Below the Seed

Entire Petri-dish cultures of *Pythium irregulare*, grown on potato dextrose agar, were placed in steam-sterilized soil in 4-inch pots at the following depths: $\frac{1}{4}$ inch, $1\frac{1}{2}$ inches and 3 inches. To ensure actively-growing mycelium, 2-day old cultures of the fungus were employed in this experiment. Twenty-five Spanish onion seeds were sown in a circle towards the circumference of each pot and were covered with three-eighths inches of soil.

TABLE 1.—SEEDLING EMERGENCE AND POST-EMERGENCE MORTALITY OF SPANISH ONIONS GROWN IN STEAMED SOIL WITH *Pythium irregulare* PLACED AT THREE DEPTHS BELOW THE SEED

Depth of infestation (inches)	Percentage				
	Emergence	Post-emergence mortality* at end of:			Stand 6 weeks after seeding
		2 weeks	3 weeks	5 weeks	
$\frac{1}{4}$	36.0	7.4	84.0	88.8	4.0
$1\frac{1}{2}$	76.0	17.0	50.0	70.1	27.4
3	89.3	0.0	12.4	30.6	62.0
Check	86.0	0.0	0.0	0.0	86.0

* Post-emergence mortality is shown as a percentage of the emergence.

TABLE 2.—WEIGHTS OF TOPS AND ROOTS OF SPANISH ONION SEEDLINGS GROWN IN STEAMED SOIL IN WHICH *Pythium irregulare* WAS PLACED AT THREE DEPTHS BELOW THE SEED

Depth of infestation (inches)	Total number of plants	Average weight in grams*		
		Entire plant	Tops	Roots
$\frac{1}{4}$	6	0.34	0.21	0.13
$1\frac{1}{2}$	29	0.63	0.46	0.17
3	91	0.42	0.30	0.12
Check	124	0.89	0.54	0.35

* Average of six pots six weeks after seeding.

The experiment provided six replications for each depth of infestation with a similar number of pots containing sterile agar to serve as controls. The soil in the pots was kept moist by sprinkling with water daily. The test was carried out in the greenhouse in late February, March and early April under environmental conditions similar to those obtaining in commercial greenhouses. The seedlings were "topped" three times during the course of the experiment. The seedling emergence and post-emergence mortality was recorded periodically and results are presented in Table 1. Six weeks after seeding all living plants were removed from the pots, washed free from soil, the tops and roots were air-dried and then weighed separately. These weights are shown in Table 2.

If reference is made to Table 1, it will be noted that, when the inoculum was placed $\frac{1}{4}$ inch and $1\frac{1}{2}$ inches below the seed, the emergence was 40 per cent and 10 per cent lower, respectively, than in the check. There was, however, no decrease in emergence when the fungus was placed at the 3-inch level. For the most part, decrease in emergence in the inoculated soils has been considered to be due to pre-emergence damping-off. *Pythium irregulare* caused post-emergence killing at all three depths of infestation (Figures 11, 12, and 13). This manifestation of the disease was not only more severe at the $\frac{1}{2}$ and $1\frac{1}{2}$ -inch levels than at the 3-inch level, but appeared earlier and typical damping-off, as expressed by a collapse of tissue at the soil line, developed. At the 3-inch level of inoculation, however, post-emergence killing was characterized by a progressive stunting, wilting and

yellowing of above-ground parts until finally, death ensued. On such plants most of the roots were found to be completely rotted soon after the first appearance of symptoms on the leaves. In many of these plants, even though extensive root necrosis developed, new roots were produced beyond the diseased area at the periphery of the bulb. Moreover, partial recovery of many affected seedlings was observed at the end of the experiment. As revealed by Table 1, in the aggregate, the closer the inoculum was placed to the seed the lesser was the stand obtained.

The weight of roots and tops was in agreement with the appearance of the plants. As Table 2 shows, the average weights of the roots and tops in the check were appreciably greater than in any of the inoculated pots. If, during the course of the experiment, "topping" had not been practised, the weight of the non-inoculated controls would have undoubtedly been still greater because more leaf growth was removed from these plants than from the inoculated plants.

Effect of Pythium Irregulare Upon Spanish Onion Seedlings of Different Ages

Since the disease appears characteristically in commercial greenhouses, where the seed is sown in steamed soil, not at the time of emergence but after the crop has made considerable growth, it would seem that the fungus enters the soil some time after the seedlings emerge and subsequently builds up rapidly. Furthermore, the results of the previous experiment, where steamed soil was infected at different depths, suggested that seedlings were susceptible for a considerable time. To ascertain the probable time of infection, plants of different ages were exposed to *Pythium irregulare* in the following manner: A 1-inch core of inoculum was inserted in a hole three inches deep in the centre of 4-inch pots of steamed soil at the time of seeding, at emergence, at 7, 14, and 21 days after emergence. The inoculum consisted of a 4 per cent mixture, by weight, of cornmeal in sand through which the fungus had completely grown. Sterile cornmeal-sand medium was added to the check pots. Twenty-five seeds were planted in a circle toward the outside of each pot and were covered with three-eighths inches of soil. In this experiment six pots comprised the test unit for each of the five inoculations and the uninoculated check. The tops of the plants were "cut back" three times during the course of the experiment. As a final measure of the effects of the fungus, all plants were removed from the pots at the end of six weeks, washed free from soil, air-dried, and the roots and tops weighed separately. Results are listed below in Table 3.

As Table 3 shows, post-emergence mortality was found to be extensive only when the fungus was introduced into the soil at the time of seeding. Seedlings that were killed showed typical symptoms of damping-off, i.e. a collapse of tissues at the ground level. All seedlings that were exposed to inoculum at the time of emergence and at later stages manifested wilting and yellowing of leaves 14 to 27 days after inoculation. The later appearance of symptoms in plants inoculated at emergence and at seven days' post-emergence than in those inoculated subsequently may have resulted from the use of inoculum which was 21 and 28 days old, respectively, in the former, whereas for all other inoculations 12- and 14-day old inoculum was used.

TABLE 3.—THE RELATION OF AGE OF SPANISH ONION SEEDLINGS GROWN IN STEAMED SOIL INOCULATED WITH *Pythium irregulare* TO THE TIME OF SYMPTOM DEVELOPMENT, POST-EMERGENCE MORTALITY, AND WEIGHT OF ROOTS AND TOPS

Time of inoculation	Percentage post-emergence mortality*	Period for symptom appearance in days**	Total number of plants	Average weight in grams		
				Entire plant	Tops	Roots
At seeding	65.0	—	23	0.46	0.31	0.15
At emergence	7.3	24	97	0.55	0.35	0.20
7 days post-emergence	1.3	27	108	0.52	0.34	0.18
14 days post-emergence	0.6	14	104	0.37	0.27	0.10
21 days post-emergence	0.0	15	111	0.41	0.30	0.11
Check	0.0	—	110	0.75	0.43	0.32

* Post-emergence mortality is shown as a percentage of the emergence.

** Period for symptom appearance is the time in days between inoculation and the first evidence of disease on above-ground parts.

Concomitant with the appearance of above-ground symptoms was a typical root necrosis. As mentioned previously, in many diseased seedlings, at least 50 per cent of the roots were rotted before any conspicuous above-ground evidence of disease was noted. The fungus was readily isolated from these necrotic roots.

As expressed in Table 3, the average weight of roots and tops was found to be considerably greater in the checks than in any of the inoculated units. This finding was in accord with the general appearance of the plants (Figure 10).

CONTROL OF THE DISEASE

In a preliminary experiment in which Arasan (50 per cent tetramethyl thiuram disulphide) was added to steam-sterilized soil, at the rate of 3.1 gm. per cu. foot, previous to seeding, evidence of the effectiveness of the treatment in the control of rootrot was obtained. This rate of application not only delayed the appearance of the disease but appreciably reduced the incidence of rootrot. Further research is being done on this phase of the disease and will be reported in a later publication.

SUMMARY AND CONCLUSIONS

In recent years a rootrot of Spanish onion seedlings, grown either in steamed or in non-steamed soil in greenhouse flats, has become of economic importance in southern Ontario. The disease appears characteristically from four to seven weeks after planting, and causes stunting, wilting, and yellowing of leaves associated with extensive root necrosis.

Isolations from diseased seedlings revealed the consistent presence of a fungus identified as *Pythium irregulare* Buis.

In infection experiments, *Pythium irregulare* was shown to be highly pathogenic to Spanish onion seedlings, causing both pre-emergence and post-emergence damping-off. The attack of older seedlings was characterized by virtually complete necrosis of existing roots coincident with wilting, yellowing, stunting, and occasionally death of all above-ground parts. In these experiments, *P. irregulare* clearly duplicated the symptoms

observed in large commercial plantings and may be considered the chief causal agent. Hence, it would appear that the pathogen invades the steamed soil in the onion flats a few weeks after seeding and that the disease develops rather quickly under normal conditions of growth.

Results of a preliminary experiment showed that Arasan (50 per cent tetramethyl thiuram disulphide), when added to steamed soil at the rate of 3.1 gm. per cu. foot, effected considerable control of the disease.

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FIELD OBSERVATIONS ON THE BLACK ARMY CUTWORM, *ACTEBIA FENNICA* (TAUSCH.), AND ITS CONTROL ON BLUEBERRIES IN NEW BRUNSWICK

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During the seasons of 1944 and 1945 the black army cutworm, *Actebia fennica* (Tausch.), destroyed many hundreds of acres of commercially grown blueberries and seriously damaged many more in Charlotte County, New Brunswick, the losses amounting to thousands of dollars. In the same years, blueberries in the State of Maine suffered very seriously from its depredations. Growers in Charlotte County had not previously experienced damage by this insect although it was reported as a pest of blueberries in Maine in 1925 by Phipps (1).

LIFE-HISTORY

As the buds of the blueberry begin to swell in early spring, the overwintering larvae emerge from the soil, crawl up the blueberry stems, and begin boring into the buds. At this time the larvae are from one-quarter to one-half of an inch in length. Rarely a very small larva has been found within a bud, suggesting that it had overwintered in the egg stage. The egg, however, has not been seen. Full growth is reached early in June, when the insect pupates in the soil to emerge as an adult in late July or early August.

NATURE OF INJURY

Very severe but inconspicuous damage may be caused to the swelling buds by the young larva, which bores through the sides of the bud scales to eat out the interior. The small, round hole in the side of the bud is not readily seen, and estimation of the prevalence of the insect in a large barren is difficult in the early stages of plant growth. Occasionally a bud scale drops from an injured bud, producing a one-sided appearance which is more easily noted. Squeezing a bud gently between the fingers will readily indicate whether it is infested. As the buds burst, injured areas of the barren become at once apparent by contrast with the greener, uninjured areas.

The larva remains hidden in the black ash and duff on the surface of the soil of the barrens during the daytime, and emerges to crawl up the stems and feed shortly after sunset. Blossom buds and open blossoms are preferred to the foliage. Usually the terminal buds are attacked first, the larva feeding on the remaining buds as it descends. Practically all damage caused during the two years of the outbreak was on areas in their first year of fruit production after the "burn". Areas in production two or more years following burning suffered very little from this insect. Indications are that the moths invariably lay their eggs on areas in "sprouts", i.e., on areas burned over in the early spring of that year.

¹Contribution No. 2642, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada.

CHARACTERISTICS OF THE OUTBREAK

The first known infestation of the 1944 outbreak was reported on May 24 on a barren in heavy full bloom. All of the blossoms on this and many other barrens were devoured two to three days later, and the green foliage was also consumed before the caterpillars pupated on May 28 and 29. On many barrens the caterpillars began marching when most of the foliage had been stripped but the marching suddenly ceased at pupation. Complete stripping occurred on many barrens in the two main producing areas of the county, one being a narrow coastal strip some 20 miles in length near Pennfield, and the other an inland area between Whittier Ridge and Tower Hill, roughly 12 miles long and five miles wide.

In 1945 the outbreak occurred in the same areas, again on barrens which were in the first year of fruit production, and which had been burned over in the spring of 1944. On smooth barrens, i.e., areas which at one time were cultivated, infestations were more or less evenly distributed throughout the area. On rough barrens moderate infestations were confined to the hummocks and knolls, the low and wet places being left uninjured. However, stripping occurred in heavy infestations on rough barrens.

During the major part of the larval period in both years of the outbreak, weather conditions were abnormal. Records for May in the two years are compared below with the average for the previous 31 years:

	Precipitation	Mean temperature	Total sunshine
	inches	° F.	hours
1944	2.08	55.0	290
1945	8.61	47.9	165
Average (31 years)	2.86	47.9	205

Although conditions for plant and insect development in 1944 must have been ideal, it is probable that the rate of development of the blueberry was more rapid than that of the cutworm, so that the plants produced heavy bloom before defoliation occurred. Under the cold and wet conditions of 1945 both blueberry and cutworm growth rates were retarded, resulting in the destruction of blossom buds with little or no production of bloom in some areas. Cutworms collected in the field early in 1945 and reared in the insectary increased in size much more rapidly than those in the field.

ESTIMATION OF PREVALENCE OF THE CUTWORM

After the experience of the 1944 outbreak it was necessary as soon as possible in the spring of 1945 to discover the distribution and prevalence of the insect in many barrens over a wide area so that measures for control could be begun before serious damage occurred.

The careful examination of individual buds before they burst is time-consuming and does not accurately indicate the location and degree of infestations. Searching the duff and debris on the surface of the soil with the forefinger or a small whisk-broom will usually result in the discovery of

a few cutworms in heavy infestations; but again the distribution and population of the insect cannot be determined. Phipps (*loc. cit.*) remarks that the grower "should visit his field with a flashlight the next warm night in order to see the worms actually at work", and remarks further that they are conspicuous. The writer found that the cutworms fed readily at temperatures as low as 38° F. during either wet or fine weather. He also noted that, though examination of the barrens with a flashlight showed many larvae feeding, many were missed because the dark colours of the worm blended with the black ash of the barren.

It was found that sweeping the areas at night with a heavy sweeping bag quickly resulted in accurate data on the location and degree of infestation. The bag was made of heavy cotton, 30 inches deep and 18 inches in diameter, and mounted on a stiff wire hoop with a handle five feet long. Sweepings made on many barrens gave data indicating that economic losses should not occur in infestations totalling fewer than 15 worms per 50 sweeps. When the total exceeded 25 worms per 50 sweeps the immediate adoption of control measures was indicated.

CONTROL EXPERIMENTS

In 1945, dusting experiments were carried out in various areas having heavy infestations as indicated by sweeping tests. Results were recorded by noting the number of cutworms collected per 50 sweeps in the various plots. The actual counting of cutworms on all plots was shortly discontinued, however, as being time-consuming and of no significant value; for all plots, with the exception of those treated with DDT, yielded collections of hundreds of cutworms per 50 sweeps, indicating no apparent control.

Four series of 0.2-acre plots were treated at different dates, the amounts per acre being indicated in brackets: 3 per cent DDT (70 lb.); 2 per cent Lethane (70 lb.); copper sulphate-calcium arsenate-hydrated lime, 20-20-60 (60 lb.); gypsum-synthetic cryolite, 70-30 (60 lb.). The first treatment (Series 1) was applied on May 9. A very heavy and untimely snow-storm two days later covered the plots to a depth of 10 inches. On May 14, as soon as the snow had melted, another series of plots (Series 2) were treated and test sweepings were made on Series 1. One sweeping of 50 strokes down the centre of each plot yielded hundreds of cutworms from all except the DDT plot; none was collected in this plot although it was swept many times. The second and two more series (Series 3 and 4), dusted on May 16 and 20, gave identical results, namely, almost 100 per cent mortality in the DDT plot and no apparent control from any other treatment. Twenty-four hours after the treatment of Series 3, great numbers of cutworms were found violently wriggling in the black ash and duff on the DDT plot. The affected worms which were collected died within 24 hours. On May 21, 3 per cent DDT dust at 40 lb. per acre and also undiluted cryolite at 30 lb. were applied on replicated plots from 1 to 3 acres in extent. The DDT again produced almost 100 per cent mortality, whereas cryolite did not give any apparent reduction.

Tests were carried out with poisoned bran bait made according to the following formula:

Wheat bran	20 pounds
Paris green	1 pound
Molasses	2 quarts

The bait was applied at 40 lb. per acre without producing any obvious effect on the cutworm population. Substitution of oil (Imperial White Oil No. 5, Visc. Saybolt 81) for the molasses did not increase the effectiveness of the bait. Many growers used the bran bait at amounts ranging from 20 to 150 lb. per acre. Sweepings on some of the treated areas, including one huge barren where the bait had been applied three times, gave large collections of cutworms, indicating little or no control.

CONCLUSIONS

1. Sweeping of the blueberry barren at night before damage becomes apparent is the most satisfactory method of determining the possible need for control of the black army cutworm.

2. Three per cent DDT dust, used at the rate of 40 lb. per acre, gave almost 100 per cent mortality of the insect. Amounts as low as 25 lb. per acre may give economic control.

3. Two per cent Lethane, 20 per cent calcium arsenate, and synthetic cryolite dusts were ineffective.

4. The application of poisoned bran bait in amounts up to 150 lb. per acre provided no appreciable control. The substitution of molasses by a light oil did not increase the effectiveness of the bait.

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BOOK REVIEW

VERNALIZATION AND PHOTOPERIODISM, by A. E. Murneek and R. O. Whyte with H. A. Allard, H. A. Borthwick, Erwin Bünning, G. L. Funke, Karl C. Hamner, S. B. Hendricks, A. Lang, M. Y. Nuttonson, M. W. Parker, R. H. Roberts, S. M. Sircar, B. Esther Struckmeyer, and F. W. Went. Foreword by Kenneth V. Thimann. Waltham, Mass.: Chronica Botanica Co.; Ottawa: Thorburn and Abbott, Ltd. XV + 196 pages, illus. \$4.50.

This symposium is of great value to all interested in the study of plant growth. The authors are well known to agronomists and plant physiologists. At the end of each section there is a comprehensive list of references and literature is cited freely throughout the text. A number of subjects are dealt with but they are allied and interdependent.

In the first section, theories dealing with low temperature treatment of seeds and the resulting responses have been clarified. The principle is emphasized that, if germinating seeds respond to low temperatures, a high or an alternating temperature and treatment in the absence of O_2 may reverse or arrest the process of vernalization. The second section deals with photoperiodism as modified by temperature and other environmental factors. The following six sections are chiefly concerned with hormones, wave lengths, nutrition and metabolism, as a means of explaining vernalization and photoperiodism in relation to flower formation. In many plants definite anatomical and histological changes occur as the plants approach the cycle of sexual maturity. Length of day in climates is regarded as a major factor in the distribution and changing of flora throughout the history of this planet. The three remaining sections, aside from the final special supplement, discuss vernalization and photoperiodism in the tropics and make preliminary observations on phenological data as a tool in the study of photoperiodic and thermal requirements of plants and the thermoperiodicity of light and temperature optima at various stages of plant growth. The special supplement in German contains studies of photoperiodicity in the tropics, the significance of daily rhythm of endogenous plants, and genetic studies of photoperiodism in crosses between Mammoth (short day) and Java (day-neutral) tobaccos. A study of this book will assist the agronomist and physiologist to assess and interpret responses of plant growth to the environment. It is recommended as a valuable guide and reference book.

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